

Chapter 11

Macroevolutionary Trends in the Skull of Sauropodomorph Dinosaurs – The Largest Terrestrial Animals to Have Ever Lived

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Idea and Aims

Geometric morphometric analysis was applied to the skull (separately in lateral and dorsal view) of sauropodomorph dinosaurs from the Mesozoic. These analyses were applied to quantify the macroevolutionary trends in sauropodomorph craniofacial form. As the early craniofacial evolution of Sauropodomorpha has been considered to be “conservative”, with all major changes to skull shape occurring within Sauropoda itself, geometric techniques are herein employed to quantify this statement. The landmark-based approach (relative warps analysis) was able to confirm this statement, albeit within the limits of the sample of this study. The morphospaces in both views demonstrate that sauropodomorphs became more divergent in terms of craniofacial form, with the sauropods occupying a distinct region of, and a greater volume of, morphospace than the “prosauropods”. Although the concordance between craniofacial form and phylogeny is statistically significant, the correlations themselves are not significant. As such, craniofacial evolution within Sauropodomorpha is “shaped” by more than just historical contingency.

Introduction

Throughout most of the Mesozoic era (250–65 Mya) sauropodomorph dinosaurs were the dominant terrestrial herbivores. They reached the biomechanical limits of terrestrial gigantism, with many species of taxa achieving sizes an order of magnitude larger than other extinct or living terrestrial animals (Sander 2000). Therefore, the question arises, how did these multi-tonne giants fuel their colossal bodies? How was it possible for there to be six or more contemporaneous species of giant

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sauropods in Late Jurassic (155–145 Mya) ecosystems? As with examples of multiple contemporaneous large carnivorous dinosaurs (e.g. Henderson 1998), resource (niche) partitioning via morphological differentiation has been posited as maintaining high biodiversity. In the case of sauropods, differentiation is concentrated on craniofacial form (although tooth crown and neck morphology are also important) (e.g. Barrett and Upchurch 1994; Calvo 1994; Upchurch and Barrett 2000; Barrett and Upchurch 2007; Upchurch et al. 2007).

Sauropodomorpha is a clade consisting of two well-known groups, Sauropoda and Prosauropoda. Recent phylogenetic analyses have convincingly demonstrating the paraphyly of Prosauropoda (e.g. Upchurch et al. 2007; Yates 2003, 2007; Yates and Kitching 2003), therefore we hereafter refer to all non-sauropod sauropodomorphs as “prosauropods” in the knowledge they do not constitute a natural group. Although the topology of the sauropodomorph evolutionary tree is still disputed in these analyses, the taxa selected in this study remain stable throughout (Fig. 11.1).

Although recent work has demonstrated the unrealised craniofacial diversity within Sauropoda (e.g. *Nigersaurus*; Sereno et al. 2007), “prosauropods” have long been considered conservative in cranial morphology, while their feeding mechanisms are still considered to be conservative (e.g. Upchurch and Barrett 2005). As

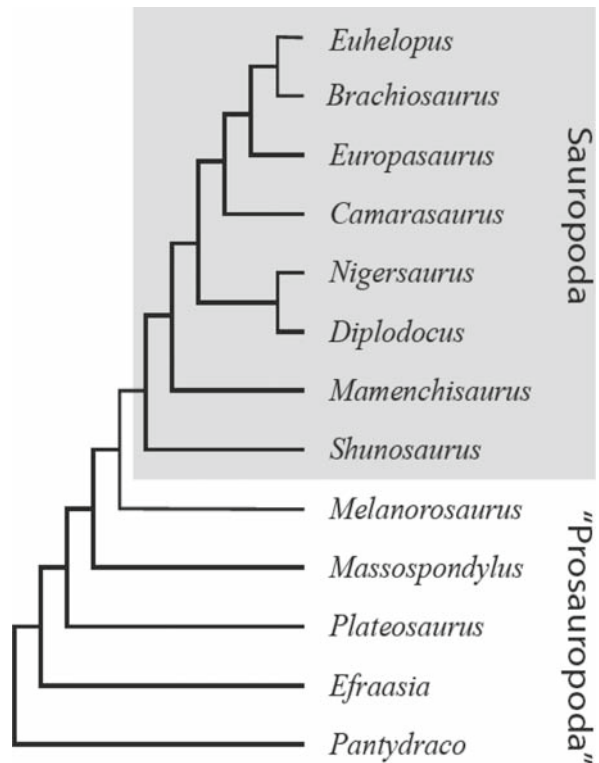


Fig. 11.1 Evolutionary relationships of sauropodomorph used in this study

recent phylogenetic analyses include numerous “prosauropods” and sauropods, we use geometric morphometrics and multivariate statistics to examine the macroevolutionary history of craniofacial form within this clade, assessing whether broad statements concerning craniofacial diversity are defensible.

Materials and Methods

The sauropodomorph cranial specimens analysed herein are all based upon photographs or reconstructions from the literature (see Larvan 2007 for the specimen list). The landmarks (Fig. 11.2, Table 11.1) were digitised using Image J vers. 1.36b (Rasband 2007).

The program tpsRelw vers. 1.42 (Rohlf 2005) was used to perform the relative warps analyses (RWA; Rohlf 1993). The first step was to perform a generalised Procrustes analysis on the landmark configurations taken from the digital images, to remove differences in location, orientation and scale (see Stayton and Ruta 2006). Once the landmarks were in Procrustes superimposed space a consensus plot (= the mean shape) was calculated. This consensus plot is the mean landmark configuration from all species in the sample. A principle components analysis was done on shape co-ordinates (see Cavalanti 2004 for the full methodology in detail).

Going from Procrustes superimposed alignment to an ordination plot involves projecting the data points (the taxa) from a curved surface on to a flat one. This can be thought of as taking one side of a globe and projecting the towns and cities onto a map. The process of projection can lead to significant distortion of the relative positions between taxa. To test for this, the Procrustes distances (distances between specimens in Procrustes alignment) were regressed against the Euclidean distances (distances between specimens on the morphospace plot) using the program tpsSmall vers. 1.20 (Rohlf 2003).

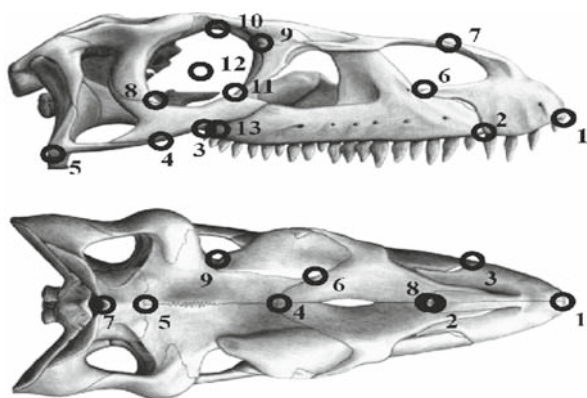


Fig. 11.2 Lateral (*top*) and dorsal (*bottom*) view of a *Melanorosaurus* skull with the landmarks taken shown (see Table 11.1) (image modified from Yates (2007))

Table 11.1 Morphometric landmarks used, with their description

Number	Skull lateral aspect	Skull dorsal aspect
1	Anterior most point along premaxilla ventral margin	Anterior most point of premaxilla along the midline
2	Premaxilla-maxilla suture along ventral margin	Posterior most point of premaxilla along the midline
3	Posterior most point along maxilla ventral margin	Premaxilla-maxilla suture along lateral margin
4	Anterior most point along quadratojugal ventral margin	Nasal-frontal suture along the midline
5	Inflexion point of quadratojugal at the mandibular joint	Frontal-parietal suture along the midline
6	Premaxilla-maxilla suture along dorsal margin	Prefrontal-nasal-frontal suture
7	Dorsal most point of the premaxilla	Posterior most point of the parietal along the midline
8	Jugal-postorbital suture along the orbit rim	Anterior most point of the nasal along the midline
9	Lacrimal-prefrontal suture along the orbit rim	Prefrontal-frontal suture along the orbital margin
10	Prefrontal-frontal suture along the orbit rim	
11	Jugal-lacrimal suture along orbit rim	
12	Centroid of orbit	
13	Posterior end of tooth row	

Four disparity metrics were calculated using all the RW scores from all axes, for “prosauro pods” and sauropods: the sum and product of the ranges and variances (Wills et al. 1994). Each metric gives an indication of volume of morphospace occupied. However, range measures quantify the entire spread of morphological variation, or the “absolute extent of bodyplan variety” (Wills 1998), whereas variance measures indicate average dissimilarity among forms. The former are more sensitive to sample size, whereas the latter are more sensitive to taxonomic practice but robustly insensitive to sample size (Wills et al. 1994). All metrics were calculated using the software program Rare (Wills 1998), and multiplicative measures were normalised by taking the 13th root. Statistical significance between the disparity of “prosauro pods” and sauropods were assessed in two ways: by the overlap or non-overlap of 95% bootstrap confidence intervals for each disparity metric (calculated by Rare with 1,000 replications) and NPMANOVA (non-parametric multivariate analysis of variance), which tests for significant differences in the distribution of groups in morphospace (Anderson 2001). NPMANOVA, the multivariate (and non-parametric) equivalent of ANOVA, was calculated in PAST (vers. 1.78; Hammer et al. 2001). One of the strengths of NPMANOVA is that as a non-parametric statistical test, it does not assume or require normality from the multivariate data.

In order to assess the fit between RW skull morphospace and phylogeny, Mantel’s test was used. From the phylogeny a simple symmetrical node-based difference matrix was collated, while Procrustes distances were calculated using tpsSmall (v1.20, Rohlf 2003) and then collated to a similar symmetrical matrix. The resulting matrices were imported into PAST (v1.78) and a Mantel’s test carried out.

Analyses

Regression of Procrustes distance against Euclidean distance for each pair of landmarks gave a high correlation coefficient with $r > 0.99$ for both cranium lateral and cranium dorsal aspect views. As such, distortion did not prevent interpretation of results from the Relative Warp morphospaces.

The first two RW axes in lateral view were deemed significant as they account for 97.7 percent cumulatively of the variance about the mean shape (Fig. 11.3). Moving across RW1, negative to positive, all landmarks move rostrally; 5 (inflexion point of quadratojugal at the mandibular joint), 6 (premaxilla-maxilla suture along dorsal margin) and 7 (dorsal-most point of the premaxilla) only slightly; whereas 8 (jugal-postorbital suture along the orbit rim) and 10 (prefrontal-frontal suture along the orbit rim) “move” considerably. In addition, landmarks 1 (anterior-most point along

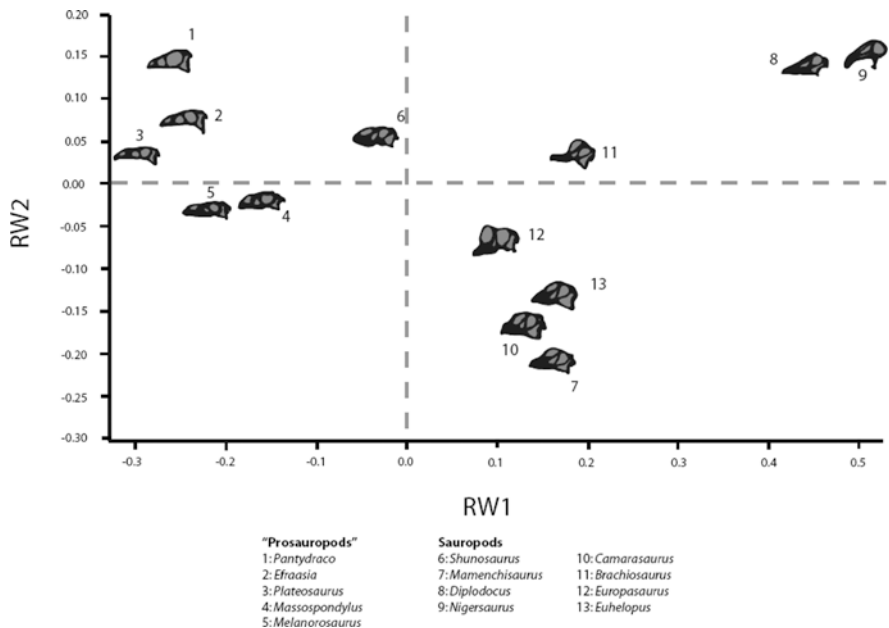


Fig. 11.3 Relative warps lateral view cranial morphology morphospace delimited by the first two axes

the premaxilla ventral margin), 2 (premaxilla-maxilla suture along ventral margin) and 12 (centroid of orbit) exhibit a downwards movement, while landmark 2 converges on landmark 1. Landmark 4 (anterior-most point along quadratojugal ventral margin) is the only one to show an elevation in position. Based on the landmark position changes, progressively positive RW1 values have a lengthened premaxilla and the quadratojugal elongating and advancing rostrally (rostral movement of the jaw joint). The second RW axis subsumes three shape variations: 1) snout elongation, 2) tooth-row shortening and 3) orbit moving up and backwards. Moving negative to positive across this axis, landmarks 1–3 (posterior-most point along maxilla ventral margin) and 8–12 are elevated, 4–7 and 13 (posterior end of tooth row) are depressed, while landmarks 1, 4, 5 and 8–12 “move” caudally and 2, 3, 6, 7 and 13 “move” rostrally.

The morphospace delimited by the first two RW axes in dorsal view (Fig. 11.3) displays separation between “prosauropods” and sauropods across RW1, with *Shunosaurus* intermediate between the two. The diplodocoids (*Diplodocus* and *Nigersaurus*) are distinguished from all other sauropodomorphs, with an elongate snout and a retracted external nares (bony hole for the soft tissue of the nostrils and olfactory senses).

The first two RW axes in dorsal view were deemed significant as they accounted for 72.6 percent cumulatively of the variation about the mean shape (Fig. 11.4). Moving across RW axis one, from negative to positive, landmark 3 (premaxilla-maxilla suture along lateral margin) advances rostrally. Landmarks 2 (posterior-

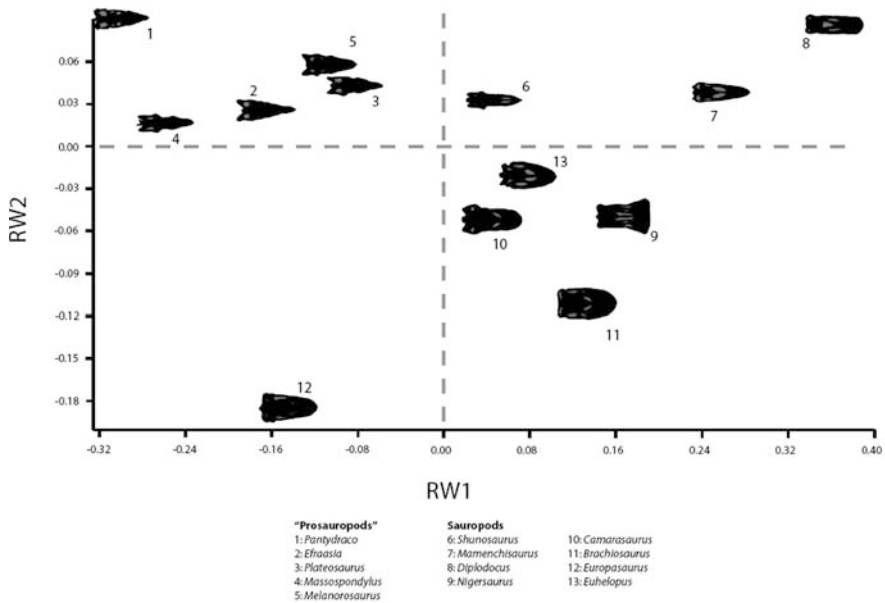


Fig. 11.4 Relative warps dorsal view cranial morphology morphospace delimited by the first two axes

most point of premaxilla along the midline), 4 (nasal-frontal suture along the midline) 6 (prefrontal-nasal-frontal suture), 8 (anterior-most point of the nasal along the midline) and 9 (prefrontal-frontal suture) all “move” caudally. The second RW axis subsumes skull narrowing and lengthening, in addition to narrowing of the premaxillae and the shortening of the nasals. Moving from negative to positive across the axis, landmarks 1 (anterior-most point of the premaxilla along the midline), 4, 5 (frontal-parietal suture along the midline), 6 and 9 are in a rostral position; whereas landmarks 2 and 8 are in a caudal position, and landmarks 3 and 9 “move” in to a medial position. Landmark 7 (posterior-most point of the parietal along the midline) does not alter position in either RW axes.

The morphospace delimited by the first two RW axes in dorsal view (Fig. 11.4) displays separation between “prosauropods” and sauropods across RW1 and RW2, with *Shunosaurus* intermediate between the two. Unlike the lateral view morphospace, the diplodocoids (*Diplodocus* and *Nigersaurus*) are not united as *Nigersaurus* has a laterally expanded snout. *Europasaurus* (the only known case of insular dwarfism within Sauropoda) is the only sauropod with negative RW1 values.

Comparing the distributions of “prosauropods” and sauropods morphospace occupation in both lateral and dorsal view achieved statistical significance (Table 11.2), meaning they occupied significantly distinct regions of morphospace.

Table 11.2 Results from NPMANOVA comparisons of group morphospace distributions from the RW scores. All results based upon 50,000 permutations. The significant p-values are in bold

“View”	Comparison	F-value	P-value
Cranium dorsal	“Prosauropod” Sauropod	4199	0.0013
Cranium lateral	“Prosauropod” Sauropod	11.93	0.0006

All disparity metrics show that sauropods are more disparate in terms of volume of morphospace occupation; however the very small sample size (“prosauropod” $n = 5$, sauropod $n = 8$) of this analysis severely limits the rarefaction profiles (Fig. 11.5). As the 95% confidence intervals consistently overlapped, statistically significance could not be achieved.

The fit between craniofacial form and phylogeny was found to be statistically significant for both dorsal and lateral view (Table 11.3). However, the correlations themselves were not significant for either view (the highest R^2 being 0.55).

Discussion

This study was primarily concerned with using a measure of morphological variation in order to quantify craniofacial macroevolutionary trends. Relative Warp Analysis was used to measure the variation in skull geometry as the deviation from a

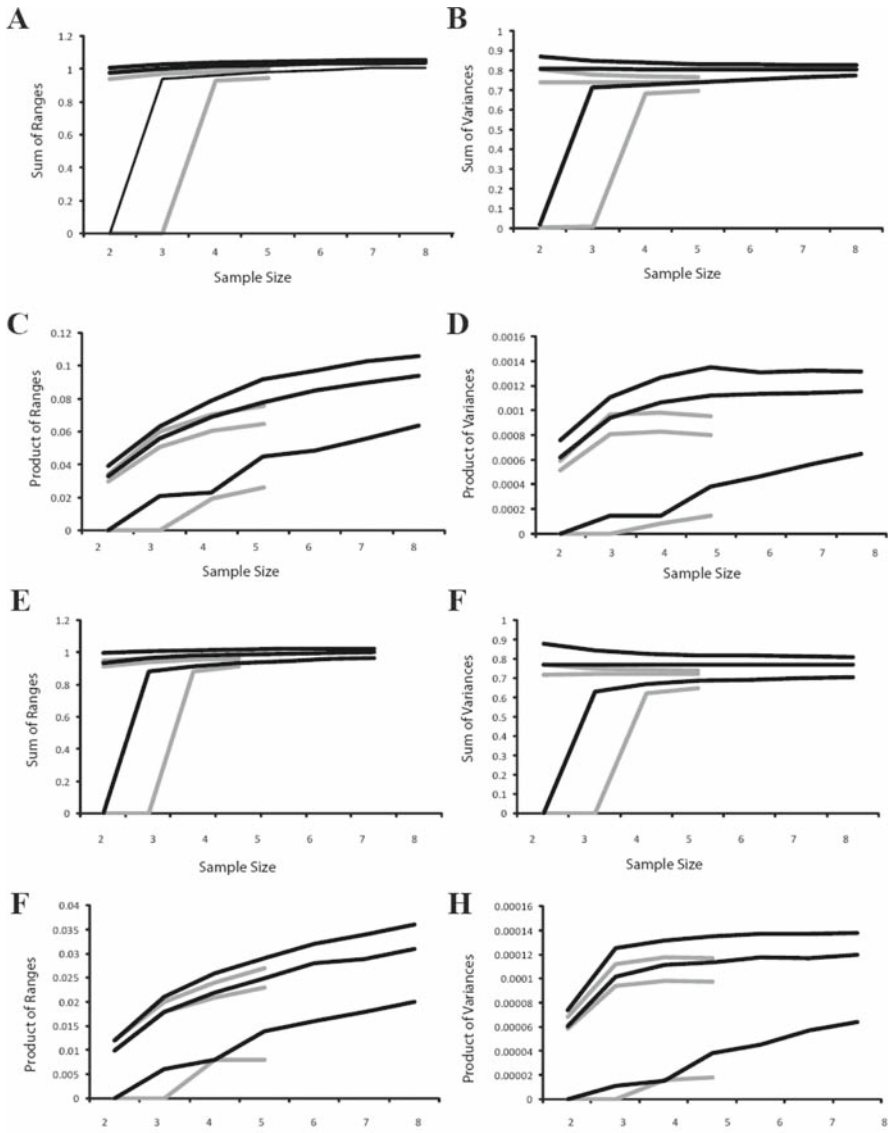


Fig. 11.5 Rarefaction profiles for all four disparity metrics (sum and product of ranges and variances) for “prosauro pods” (in grey) vs sauropods (black). The profiles for the skull dorsal view (a–d) and lateral view (e–h) are shown with the mean value and 95% confidence intervals as three separate lines

mean shape of the landmark positions. Herein, geometric morphometric techniques delineated “prosauro pods” and sauropods in morphospace, although small sample size meant that quantifying volume of morphospace occupation (disparity metrics) failed.

Table 11.3 Correlation results from the Mantel's test of the Procrustes and phylogenetic distances. All results based upon 5,000 permutations. The significant p-values are in bold

"View"	R ²	P-value
Cranium dorsal	0.35	0.01
Cranium lateral	0.55	<0.01

Relative warps morphospaces for both lateral and dorsal view of the cranium could distinguish clades within Sauropodomorpha. The separation between "prosauropods" and sauropods can be distinguished in their cranial morphology. The prosauropods have lower, more tapered snouts, narrowing towards the tip, whereas sauropods have taller skulls with more robust snouts. The dorsal view shows this varied design, with a clear distinction of "prosauropods", but a large degree of variation within Sauropoda. The basal sauropods (*Shunosaurus* and *Mamenchisaurus*) have a similarly slender appearance, whereas the neosauropods (all taxa more derived than those two, see Fig. 11.1) exhibit a broadening in the snout, resulting in a generally even width from posterior to anterior end of the skull.

The comparatively small morphospace occupied by the "prosauropods" provides very tentative support for the hypothesis that they were more conservative in craniofacial form (and presumably function) and that the sauropods were much more diverse, as shown by their greater morphospace occupation.

With the exception of the dorsal view, diplodocoids are significantly separated in morphospace from all other sauropodomorphs. This is due to their distinct craniofacial form (e.g. elongate snout, retracted external nares), which is possibly related to the feeding strategies hypothesised for this clade (branch stripping and precision biting; Barrett and Upchurch 1994, 2007; Calvo 1994).

Although broad trends within sauropodomorph craniofacial evolution can be discerned, the low correlation between form and phylogeny suggests that phylogenetic inertia has a limited impact upon craniofacial form. This refers to the notion that constraints imposed by phylogenetic history could potentially refrain the skull from reaching its functional optimal.

Conclusions

Geometric morphometrics analyses of skull landmark configurations (lateral and dorsal view) were able to delineate sauropods from "prosauropods". Both views demonstrate that sauropodomorphs became more divergent in terms of craniofacial form throughout the Mesozoic, most especially the sauropods. A clear evolutionary trend towards cranial robustness in sauropods is supported by morphometrics, which also supports the general craniofacial conservativeness of the "prosauropods". Evaluating statistical significance of the distribution and disparity for sauropods and "prosauropods" demonstrate that sauropods occupy a distinct

region of morphospace, and have greater dispersal within morphospace. In addition, there is a statistically significant correlation between craniofacial form and phylogeny; however the correlations themselves are not highly significant.

Although this macroevolutionary study has begun the quantitative elucidation of sauropodomorph evolution, the key problem to our continuing understanding of sauropodomorph craniofacial evolution is the scarcity of well-preserved skulls. Recent studies have shown not only the unrealised cranial diversity of sauropodomorphs (e.g. Sereno et al. 2007), but tooth-crown gross morphology is also highly diverse (e.g. Upchurch and Barrett 2000) and that osteological correlates for structures like a fleshy cheek are known for “prosauropods” and early sauropods (Barrett and Upchurch 2007). Clearly, there are many more exciting discoveries to be made.

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