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MORPHOLOGIC AND ONTOGENETIC PATTERNS IN ELASMOSAUR NECK LENGTH, WITH COMMENTS ON THE TAXONOMIC UTILITY OF NECK LENGTH VARIABLES

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ABSTRACT

Elasmosaur cervical vertebrae are common fossils, but their taxonomic utility is limited due to a lack of understanding concerning their shape within and among taxa. In this paper, we analyze data from complete elasmosaur necks in an attempt to quantify and understand the variation in centrum dimensions. In accord with previous studies, variation in cervical centrum shape is found to stem from at least three sources: ontogeny, intracolumn variation, and intercolumn or taxonomic variation. Ontogenetic variability seems reminiscent of that seen in *Cryptoclidus*, with an overall positive allometry in the length of all centra that is accentuated in the mid-cervical region. In adult elasmosaurs, the longest centra occur in the middle of the neck, and centra in this region are longer than those at either end. This pattern yields a distinctively bowed shape curve when a shape metric such as VLI or PC2 score is graphed against vertebral position. Centrum length shows minor variation from centrum to centrum in all elasmosaurs, but a small group of extreme, 'elongate' animals have a much higher degree of variability. Animals in this group show significant changes in centrum dimensions late in ontogeny. The taxonomic utility of centrum measures is limited because there is no single pattern of centrum shape common to all taxa; variability is the rule, and therefore caution is necessary when using dimensions to diagnose taxa. There do seem to be two morphotypes of elasmosaurs, however. The first is a relatively conservative group with centrum dimensions similar to those of *Brancasaurus*, and that achieves a long neck by adding vertebrae. A second, elongate group has centra that are very long, and there is great variability from one centrum to another in the same column. Surprisingly, the number of cervical centra is not a highly variable trait in most elasmosaurs. The elongate taxa appear to be restricted to the Western Interior Seaway in the Late Cretaceous, although there is some indication that *Tuarangisaurus* might be elongate as well. In general, elasmosaur vertebrae have some taxonomic utility, but only at the extremes of their shape range, if the specimens are adults, and only if their position in the column is known with some certainty.

INTRODUCTION

Elasmosaurs have always been puzzling animals, beginning with E. D. Cope's infamous placement of the head of *Elasmosaurus platyurus* at the tip of the tail in his first reconstruction (1869). Cope might be excused for his mistake given that an animal with 71 cervical vertebrae was unprecedented at the time of its discovery. While elasmosaurs have now been found on every continent including Antarctica (Persson 1963, Chatterjee and Small 1989), our understanding of these enigmatic animals is still under constant revision, with new interpretations of their morphology and paleoecology appearing recently (O'Keefe 2001a, O'Keefe and Carrano 2005). The membership and relationships of the family Elasmosauridae have also been the focus of recent research attention; the new taxa *Eromangasaurus carinognathus* (Upper Albian of Australia, Kear 2005) and *Terminonatator ponteixensis* (Upper Campanian of Canada, Sato 2003) have been described, while the New Zealand taxon *Mauisaurus haasti* has been redescribed (Hiller et al. 2005). These works have markedly improved our knowledge of elasmosaur anatomy.

However, this welcome flurry of activity on elasmosaurs contains a conspicuous absence of consensus concerning the relationships within the group. Few doubt that the Elasmosauridae is a member of clade Plesiosauroidea (Welles 1943, defined cladistically by O'Keefe 2001b), comprising the most extreme examples of long neck length within the clade of long-necked plesiosaurs. But the recent phylogeny of Gasparini et al. (2003) places the aberrant Cretaceous taxon *Aristonectes* within the Elasmosauridae, a finding at odds with the results of O'Keefe (2001b, 2004), as well as Kear (2005). Gasparini et al. also support the traditional placement of *Muraenosaurus* within the Elasmosauridae, while O'Keefe (2001b, 2004) and Kear (2005) both find this taxon related more closely to the cryptoclidids. The analyses of Kear and O'Keefe utilized much larger character sets than that of Gasparini et al., but the question of elasmosaurid ingroup membership clearly lacks consensus (for further discussion of the status of *Aristonectes* see O'Keefe and Wahl 2003, Kear 2005).

The recent doctoral thesis by Sato (2002) comprises the first concerted attack on the problem of elasmosaur relationships. Sato does a very thorough job of character analysis and OTU analysis, clarifying many problems and overgeneralizations present in the analysis of O'Keefe (2001b, 2004), and also adding many elasmosaur taxa not included by that author. Unfortunately the phylogenetic analyses of Sato lack a robust topology; Sato demonstrates how the inclusion and exclusion of characters and taxa lead to major changes in the resulting topologies. Some findings from other workers are replicated, such as the grouping of *Muraenosaurus* with cryptocliedoids and outside of traditional elasmosaurs. However, the important taxon *Brancasaurus*, found to be a primitive elasmosaur by O'Keefe (2001b, 2004) and Kear (2005), occupies an extremely basal position in most of Sato's trees. If this position is correct, it renders O'Keefe's (2001b) phylogenetic redefinition of Elasmosauridae nonsensical. Neither Sato nor O'Keefe have studied the *Brancasaurus* material first-hand, however, and the emerging uncertainty over its affinities makes examination of the fossil a critical priority. Given this uncertainty, and the instability of ingroup nodes in Sato's trees as well, it is fair to state that elasmosaur systematics-- in terms of both taxonomic inclusion and ingroup relationships-- are in a state of flux.

The use of cervical centrum dimensions in elasmosaur taxonomy has a long history. Welles (1943, p. 162) used the ratio of cervical centrum length to height in an attempt to differentiate between *Thalassomedon haningtoni* and *Styxosaurus snowii*, and pointed out that centrum length changed differently along the column in the two taxa. In a later publication (Welles 1952), the same author treated a related set of ratios-- essentially centrum length vs height and width-- in a larger set of taxa, and concluded that the ratios were highly variable, with variation arising from at least three sources. The first source was variation along the column within an animal, the second was ontogenetic variation within the same taxon, and the third was true taxonomic variation. Welles demonstrated that centrum ratios could be used to differentiate between plesiosauromorph and pliosauromorph taxa, but did not attempt to tease apart the three contributing factors for use within the Elasmosauridae.

The next advance in the study of plesiosaur centrum proportion came with Brown (1981), who introduced the Vertebral Length Index, or VLI, as a single-value metric to express the relative length of centra. In doing this Brown tacitly acknowledged that centrum dimensions in width and breadth are fairly constant, at least relative to the great variation in centrum length. The VLI is calculated in the following manner:

$$VLI = 100\left(\frac{L}{(H+W).5}\right) \qquad \text{Eq. 1}$$

With H referring to centrum height measured on the posterior face, W referring to width on the same face, and L referring to length on the ventral midline. The VLI is therefore a ratio of the length of the centrum to the average diameter of its posterior face, and has several advantages. It contains an approximate size correction and therefore allows analysis of centrum shape among vertebrae of different sizes, and it expresses shape as a single number that captures the most interesting aspect of centrum variation (length), facilitating graphical and other analyses.

Brown graphed the VLI for an ontogenetic series of three specimens of *Cryptoclidus eurymerus*, a common Oxford Clay (Callovian) taxon of generalized cervical dimensions. He concluded that ontogenetic variation in centrum length was pronounced, with cervical VLI increasing by as much as 20 percentage points between juvenile and old adult animals. A more subtle pattern also emerges, one that becomes much more pronounced in elasmosaurs. The pattern is that cervicals in the mid-anterior and middle of the neck increase more in relative length than do centra at either end of the cervical series. Ontogenetic change in relative centrum length is therefore quite complex in *Cryptoclidus*: there is an overall positive allometry in centrum length, but the magnitude of this allometry varies over the column, so that mid-anterior and middle cervicals become relatively longer than centra at either end. However, the use of VLI poses several potential problems. It is unknown how VLI responds to changes in body size, and it obscures possible covariation in the width and breadth of the centra. One goal of this paper will therefore be the evaluation of VLI in order to establish its suitability as a metric.

The more general goal of this paper is to contribute to the resolution of elasmosaur relationships by performing a thorough character analysis of several features derived from elasmosaur cervical vertebrae. That all elasmosaur necks are 'long' is well known; what is less well known is the mechanics of producing a long neck. Does neck length increase by the insertion of additional vertebrae, or by the elongation of the centra that already exist? Is neck length correlated with body size, and how does neck length change over ontogeny? Obviously, without a phylogenetic framework one cannot discuss the evolutionary transitions among taxa; here we will attempt to resolve a more simple question, namely the covariation between various measures of elasmosaur cervical vertebrae. We first characterize how centrum shape changes ontogenetically, taxonomically, and within a single column in an attempt to put some constraint on the amount of shape variability one must observe to infer taxonomic differences. We also explore the covariation between various cervical measures to ensure that cladistic characters based on centrum dimensions are not redundant. Lastly, we attempt to evaluate the taxonomic utility of single centra, or short series of centra. Fragmentary vertebral series are very common elasmosaur fossils, and identification of diagnostic centrum proportions would be a great aid in identifying taxa. However, it is not known whether truly diagnostic proportions even exist. We attempt to answer these questions by analyzing data from complete, well-preserved elasmosaur necks, in the hope that understanding how centrum proportions vary within the same animal will constrain their diagnostic utility.

MATERIALS AND METHODS

To determine how various centrum measurements are correlated, we analyzed data from complete, or largely complete, elasmosaur necks culled from the literature. Much of these data came from Welles (1943, 1952, 1962), but several other authors were consulted as well (see appendix), while the data for the New Zealand taxon *Mauisaurus* is original to this study. The core data set contains seven genera of adult elasmosaurs: *Styxosaurus* (two specimens), *Thalassomedon*, *Elasmosaurus*, and *Hydralmosaurus*, from the Cretaceous Western Interior Seaway, *Hydrotherosaurus* from California, *Mauisaurus* from New Zealand, and *Callawayasaurus*, from Colombia. Taxonomy of American elasmosaurs follows Carpenter (1999). The age of most genera is latest Cretaceous (Santonian or younger, Everhart 2005), although *Thalassomedon* is Cenomanian and *Callawayasaurus* is Lower Aptian. We have also included the controversial taxon *Brancasaurus brancai*, from the Berriasian of Westphalia (Wegner, 1914); whatever its relationships it is certainly more primitive than the derived elasmosaurid taxa in the data set and will be used for comparison. We have also included data from two juvenile elasmosaurs. One is the rather short-necked Californian elasmosaur *Aphrosaurus furlongi* (CIT 2832, Welles 1943), and this fossil contains a complete cervical series. We have also included the very immature *Leurospondylus ultimus* (AMNH 5261, Brown 1913), from the Edmonton Group, Alberta. This fossil possesses only a partial cervical column, but is notable for its extreme youth and is included to shed light on ontogenetic change in elasmosaurs (see Sato and Wu, 2006). One specimen that is not included is the juvenile referred to *Morenosaurus stocki* (CIT 2749) by Welles (1943:171); this specimen has a complete cervical series and would be very useful, but data are unavailable in the literature even though the cervicals, unlike the skull, are prepared (Sato pers. com.). Lastly, one of the *Styxosaurus* specimens included, the holotype of *"Alzadasaurus" pembertoni*, is larger than the other, and while the smaller *Styxosaurus* is not a juvenile, it is probably from a sub-adult or adult of younger age than the larger specimen. The larger specimen will be referred to as *Styxosaurus 'A'* below.

The data used in this study comprise the three measures of cervical centra used in the calculation of the VLI and normally recorded by elasmosaur workers, namely centrum length, breadth, and height, measured in millimeters. These three variables were recorded for all available cervical centra save the atlas and axis, which were excluded due to their atypical morphology. In general, only axial columns in which the positions of the centra were known with certainty were used, and these positions were also recorded, as was the total number of cervicals in the neck. The last cervical was taken as the last vertebra in which the rib articulation was carried solely on the centrum, rather than partially on the neural arch (following Seeley 1877 and subsequent authors). Only dimensions of complete, relatively uncrushed centra were included, so that some columns contain measurements from all vertebrae, while others have a scattered sample from along the column. In some cases this renders the resulting variables and indices suspect; for instance, the primitive taxon *Callawayasaurus* is missing measurements from both ends of the column, while *Aphrosaurus* is missing C49-C57. As long as the cervical series is sampled evenly from all parts of the column generalizations should be safe; however, in the case where one or both ends of the column are missing generalized statistics might be misleading. In the captions to the figures we note which taxon values may be skewed by poor sampling, and also discuss this further below.

Several analyses were performed on the data set. The first was a Principal Components Analysis (PCA) on the entire set of centrum measurements, comprising 382 complete centra from 11 taxa, with no missing data. The raw data were transformed to natural logarithms to treat for the log-linear relationships common in biological data with a large size range, and to partially treat for deviations from normality. The correlation matrix was used in the PCA due to heteroscedasticity in the variances of the three variables (for discussion of the log transform and general PCA techniques see O'Keefe 2002 and references therein). Principal component eigenvalues and loadings are reported in Table 1, while scores from this analysis are plotted in Figures 1 and 2.

TABLE 1. Principal Component Analysis results for the core data set, 382 cervical vertebrae from 11 specimens. The analysis was performed on the correlation matrix of natural logarithm-transformed data.

Variable	**variance (lnx)**	**lnPC1**	**lnPC2**	**lnPC3**
Length	0.235	0.957	0.286	-0.036
Breadth	0.238	0.981	-0.092	0.170
Height	0.207	0.972	-0.190	-0.136
Eigenvalue (%)		2.825 (94.2%)	0.126 (4.2%)	0.049 (1.6%)

The second set of analyses performed were a series of Reduced Major Axis (RMA) regressions, among various permutations of the taxon-average Geometric Mean (GM), average PC2 scores or statistics calculated from them, and the total number of cervical vertebrae in each taxon (Table 2). The use of the GM as a size proxy is the recommend course in investigating correlation between size and shape, as PC 1 does not contain only size variation, and while it is a good heuristic representation of body size it is not advisable for use in regression (Jungers et al., 1995). We therefore compared several statistics with this measure of body size to search for correlations among taxa, to discover if shape changed in a predictable way with size. For these analyses, however, we used only the sample of complete adult elasmosaurs (n = 8), so the statistical power of the regressions was not high. We also calculated several summary statistics for the VLI metric for each adult elasmosaur, including the coefficient of variation (see Sokal and Rohlf 1995; Table 3). The use of GM, or PC1 score for that matter, as a size proxy should be taken as approximate. The data set contains only neck centrum dimensions, so any 'body size' variable computed from these data really concerns centrum size rather than whole body size. However, the magnitudes of the size estimates in this paper are intuitively correct (i.e. small taxa like *Brancasaurus* and the *Aphrosaurus* juvenile have low scores on the size variables), and should be a decent proxy for overall body size.

In a subsidiary analysis (see below), we determined that the VLI is a surprisingly good proxy for lnPC2 score. On that basis, we plotted the VLI along the cervical series for various taxa to illustrate observed patterns. These plots appear in Figures 3, and are meant to serve as heuristic aids for visualizing patterns in centrum variation. In Figure 4 we present histograms of four possible variables one might use to make taxonomic assignments among elasmosaur centra. Lastly, Figure 5 plots the average centrum shape for the eight adult elasmosaur taxa, and is included to make a point about biogeographic distribution of neck length.

RESULTS

Results of the PCA are reported in Table 1 and illustrated in Figures 1 and 2. Principal Component 1 accounts for the vast majority of the variance in the data set, as one might expect given the very large range in size among both taxa and centra within taxa. Centrum length, width, and height all have high positive loadings on PC 1, which is also consistent with PC 1 largely reflecting a size factor (for discussion see O'Keefe 2002, O'Keefe and Carrano 2005). We therefore treat the scores of centra on PC 1 as a proxy for centrum size, and PC 1 scores are plotted versus vertebral number in Figure 1. Schematics of representative vertebrae are also depicted on this figure to show relative size and shape in various regions of the plot. Several patterns are immediately apparent in this plot; the most obvious is that centrum size increases from head to trunk in all plesiosaur taxa, including *Brancasaurus* and the two juvenile elasmosaurs. This is a pattern common to plesiosaurs in general, and is obvious by inspection of any mounted skeleton. However, it is worth noting that the size increase is quite smooth in all taxa, with no obvious breaks or steps. Size increase is most rapid near the head, and then shallows out toward the caudal end of the cervical series, with centrum size almost constant over the last 10 or 15 percent of the column in all taxa; in this region the diameter of centra actually continues to increase, but length shortens, so that aggregate size is constant. Among adult elasmosaur taxa, anterior cervical size is more similar than posterior size. As a generalization, posterior neck and body size varies much more than does head or anterior neck size in elasmosaurs.

Scores for PC2 are plotted versus vertebral position in Figure 2, along with representative schematics of vertebral centra to illustrate different regions of the plot. In this figure all centra are scaled to the same size to highlight shape differences. We interpret PC2 as a shape axis, because the length variable loads strongly positive on this axis, while measures of height and width load negatively. The width loading is strongly negative on this axis, while the height measure is less so; this yields an axis in

TABLE 2. Reduced major axis linear regression coefficients and levels of significance between measures of eight adult elasmosaur necks. Slopes not reported due to lack of significance. Variables are: $\overline{GM}$, average taxon geometric mean for three cervical centrum measures; lnPC2$_{\mathrm{max}}$, maximum taxon PC2 score; lnPC2$_{\mathrm{range}}$, taxon range of PC2 scores; $\overline{\ln PC2s}$, average taxon PC 2 score; Totcerv, number of cervical vertebrae. The variable $\overline{GM}$ is a proxy for body size, while $\overline{\ln PC2s}$ is a proxy for centrum shape, with higher positive scores indicating more elongated centra, and is essentially equivalent to VLI, but is more statistically justifiable.

Comparison	R^2	p - value
$\overline{GM}$ vs. $\overline{\ln PC2s}$	0.012	0.792
$\overline{GM}$ vs. lnPC2$_{\mathrm{max}}$	0.008	0.836
$\overline{GM}$ vs. lnPC2$_{\mathrm{range}}$	0.224	0.237
$\overline{GM}$ vs. Totcerv	0.062	0.554
$\overline{\ln PC2s}$ vs. Totcerv	0.203	0.262
lnPC2$_{\mathrm{max}}$ vs. Totcerv	0.398	0.093
lnPC2$_{\mathrm{range}}$ vs. Totcerv	0.270	0.187

which high positive scores correspond to long centra with a circular cross-section, while high negative scores correspond to short centra with a strongly ellipsoidal cross section.

The variation in centrum shape along the column is quite interesting, with several patterns emerging. The first is that centrum length seems to increase with positive allometry over ontogeny. This finding is provisional, because we lack a full ontogenetic series from any single taxon. However, the column for the *Aphrosaurus* juvenile, and the partial column of *Leurospondylus*, score low on PC2, and this is most obvious in the middle of the column. Unfortunately it is impossible to calculate exactly how much the length of *Aphrosaurus* centra increase because a complete adult column in not known; however, the posterior centra known from the adult specimen are plotted in Figure 3, and the difference is of similar magnitude as that recorded by Brown (1981) for *Cryptoclidus*. We therefore infer that centrum length is positively allometric in elasmosaurs as well. Another feature of the *Aphrosaurus* curve is that it is relatively flat. Scores for mid-cervical centra are almost identical to those for the anterior part of the column. Again this is similar to Brown's findings for the juvenile *Cryptoclidus*; in *Cryptoclidus* ontogenetic length increase was most pronounced in the anterior-middle and middle cervicals, and this seems to be the pattern in elasmosaurs as well. This conclusion rests on the assumption that the *Aphrosaurus* juvenile condition is similar to the juvenile condition in other elasmosaurs, and so should be taken with the proverbial grain of salt. However, stronger support for this pattern is seen in Figure 2, where the larger (and presumably older) of the two *Styxosaurus* specimens shows a marked increase in relative centrum length in the mid-cervical region.

Several other features in Figure 2 are remarkable. The first is simply the variation along the column in some elasmosaurs, especially those with very long centra such as *Elasmosaurus* and *Styxosaurus 'A'*. Cervical centra in these animals vary greatly in length, but there is no obvious pattern to this variation, either within or among taxa. In fact, animals such as *Brancasaurus* and *Mauisaurus* have a fairly smooth curve of vertebral shape (Figure 3), with relatively short centra near the head transitioning gradually to longer centra in the mid-cervical region, and then shortening again near the trunk. (This pattern is also probable for *Callawayasaurus*, although data is limited as that taxon is missing C3-C9 and C53-C58, thereby obscuring the shortening at both ends of the column). A rather smooth, humped pattern is characteristic of most elasmosaurs in Figure 2, but contrasts with that of *Elasmosaurus*, where the curve is accentuated and varies erratically along the column. This is also true of *Styxosaurus 'A'*, the other specimen in the data set with very long centra, but is much less marked in the more juvenile *Styxosaurus*. The possible significance of this pattern is discussed below.

Scores on lnPC2 therefore have obvious utility for interpreting shape variation along the vertebral column in elasmosaurs, and several complex patterns emerge. However, PC scores are not necessarily intuitive numbers in themselves, whereas the VLI is a known metric that is both easy to calculate and relatively intuitive. We therefore explored the correlation between VLI and scores on lnPC2. Calculating a regression line between the two metrics is statistically suspect because the metrics are not independent, being extractions from the same data set. However, we performed the regression anyway as a back-of-the-envelope calculation to check the agreement of the two metrics, and calculated an R^2 value of .974. The line of regression is very tight, with a rather slight pattern in the residuals due to the log transformation in the lnPC2 score. We also ran a non-parametric Spearman rank correlation test as a more formal test of correspondence, and significance here was also extremely high. The traditional ratio VLI therefore seems to be a good proxy for lnPC2 score, a shape variable arrived at by more formal statistical means, and given its simplicity the VLI metric is probably preferable. In retrospect this finding is not surprising given the loadings of the three variables on lnPC2; a high positive length loading contrasting with negative loadings for width and height essentially replicates the ratio at the core of the VLI, and so both metrics contrast centrum length with centrum face dimensions. It is interesting to note that the regression between

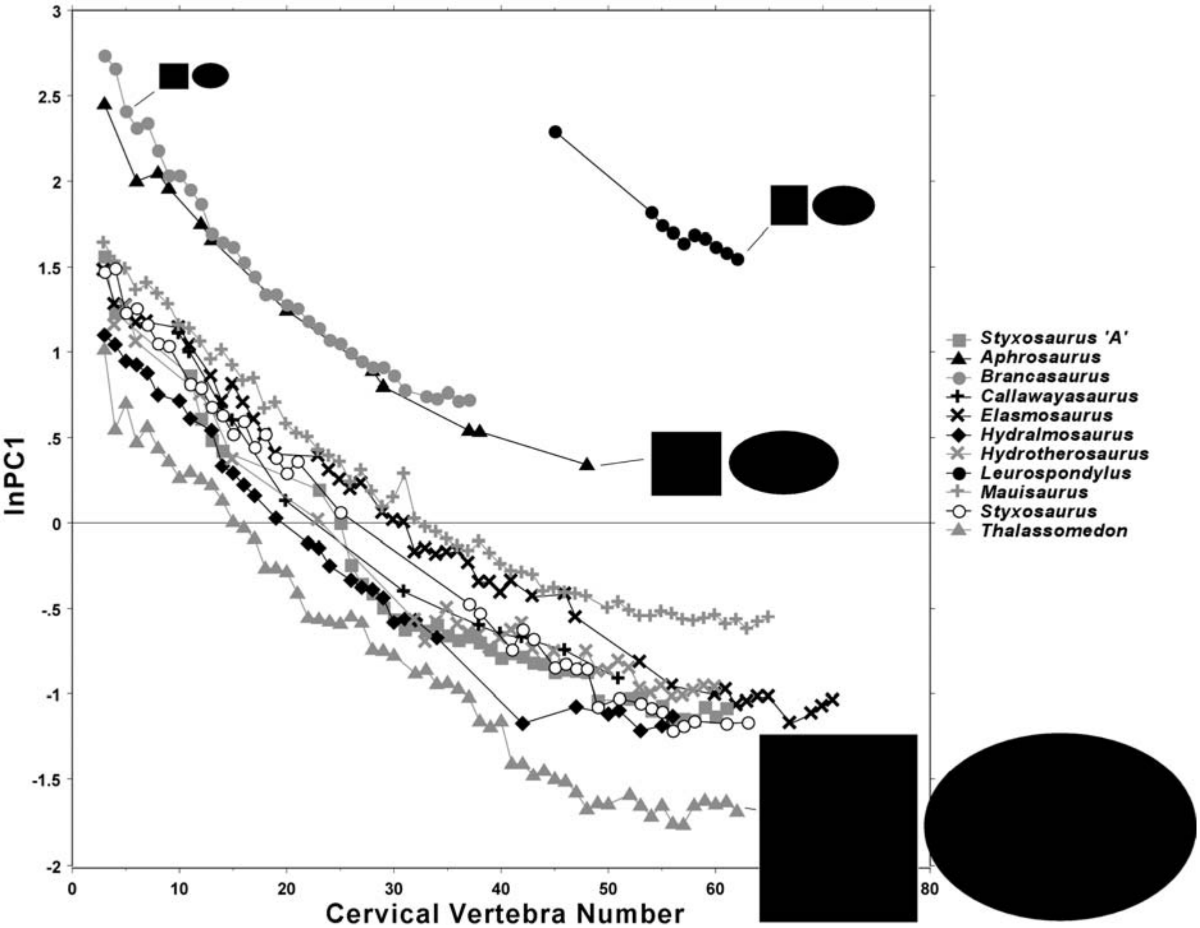

FIGURE 1. Scores for elasmosaur cervical vertebral centra on PC 1 of ln-transformed data. The abscissa plots the position of each centrum in the column. Schematics represent relative sizes of indicated centra; blocks on the left represent a side view and show length and height, while the ovoids represent the posterior centrum face and show height and breadth. Principal Component 1 is a proxy for centrum size; small centra are near the top of the figure, large ones near the bottom. Note that the *Aphrosaurus* column is missing centra from the posterior end.

VLI and PC2 score, without the logarithmic transform, is much less satisfactory, yielding an R^2 value of only .86. This effect is probably attributable to marked right skewness in the distributions of height and breadth, a lack of normality that would interfere with the ordination. The log-transform treats for this skewness.

Figure 3 comprises plots of VLI versus vertebral position for six representative taxa. Comparison between these plots and Figure 2 reveals the close correspondence between VLI and lnPC2 score. The six plots given here are included to illustrate general patterns among taxa rather than within each vertebral column. The cervical series of *Brancasaurus* is intended to represent the primitive condition for elasmosaurs, based on its phylogenetic position as the most primitive elasmosaur in O'Keefe (2001b, 2004). However, if this phylogenetic position is incorrect, *Brancasaurus* is still a primitive plesiosauroid relative to derived elasmosaurs, and so will serve for comparison. *Brancasaurus* possesses 38 cervicals, a modest increase over the 28-32 thought to be primitive for plesiosaurs as a clade (Brown 1981). The cervical centra are also more elasmosaur-like than those of *Cryptoclidus* in length; the average VLI for the whole column in *Brancasaurus* is 94, while in *Cryptoclidus* it is about 80 (inferred from Brown 1981, Figure 13). Among true elasmosaurs, the juvenile *Aphrosaurus* has an average VLI of 91. This is similar to the value for *Brancasaurus* but less than most adult elasmosaurs, and this may reflect positive allometry is centrum length, as noted above. Another indication of this allometry is the partial neck of a juvenile of *Mauisaurus* (Wiffen and Moisley 1986); the average of the five most anterior of these centra is about 80, twenty VLI points lower than the adult average for this taxon (101), and centrum 20 is even shorter.

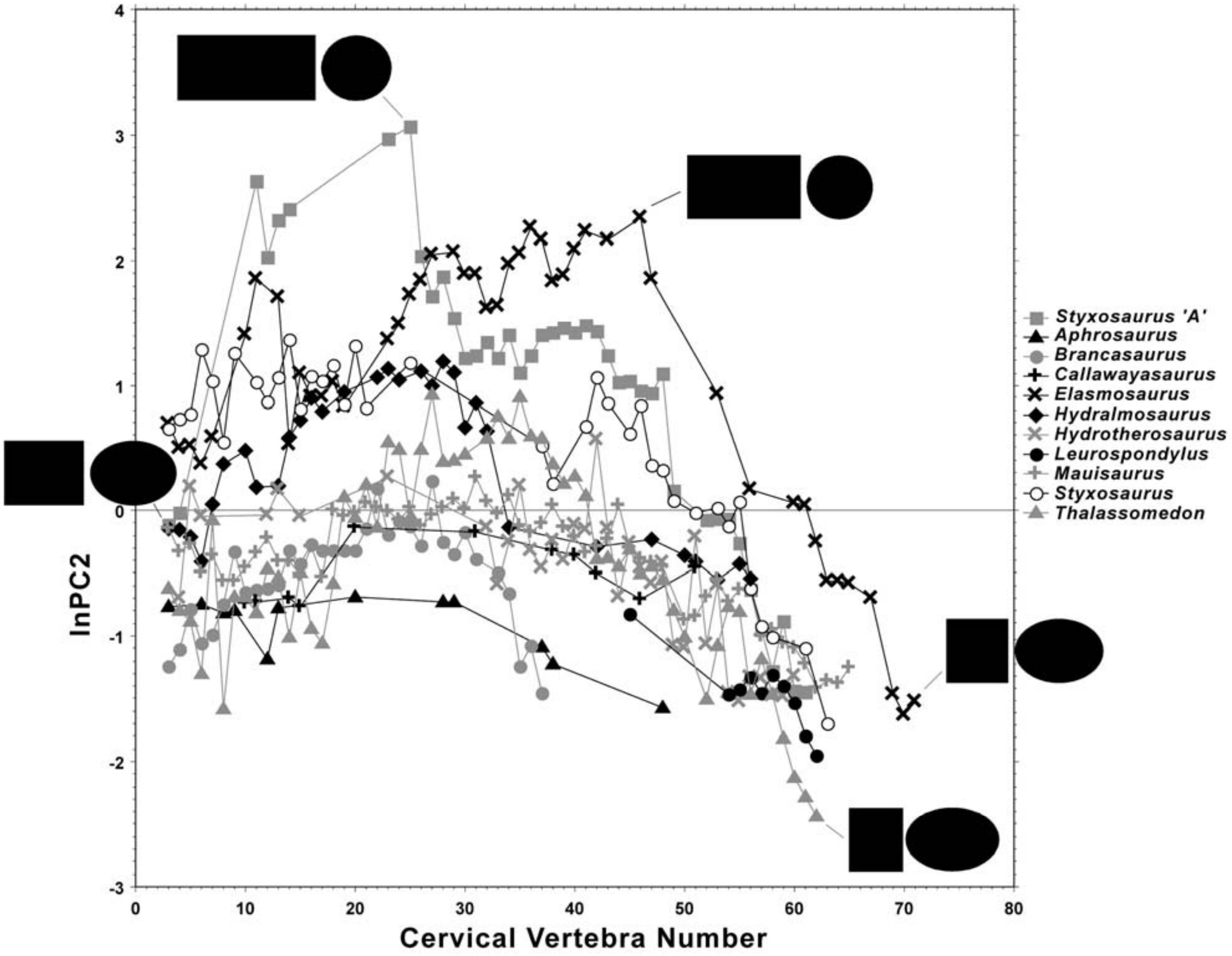

FIGURE 2. Scores for elasmosaur cervical vertebral centra on PC 2 of ln-transformed data. The abscissa is the position of each centrum in the column. Schematics represent relative shapes of indicated centra; blocks on the left represent a side view and show length and height, while the ovoids represent the posterior centrum face and show height and breadth. Long, round centra are near the top of the plot, while short, broad centra are near the bottom.

VLI curves, like PC2 score curves, therefore carry a lot of information about variability in the vertebral column, and it would be desirable to bring this to bear on taxonomic questions. We therefore attempted to establish if lnPC2 score statistics covaried with other variables of interest, such as body size, number of cervical vertebrae, or the anterior neck vertebrae (given that elasmosaur skulls are often found with short anterior cervical series). We chose to use the variable lnPC2 rather than VLI because VLI is a ratio, with complex statistical properties, while lnPC2 is a linear combination. The lnPC2 variable is also uncorrelated with the lnPC1 size estimator, so it is permissible to perform regressions between scores derived from these variables (for discussion see O'Keefe and Carrano 2005).

The results of this set of linear regressions appears in Table 2, and are remarkable for the lack of correlation between various centrum measures and body size. Even though sample size is low (n=8), strong correlations between body size, number of vertebrae, vertebral length, and other measures should still be apparent. However they are not; body size appears to be largely independent of the number of cervicals and of their shape. The only marginal correlation identified was between the total number of cervicals and the maximum length of those cervicals; this regression was not significant, but might prove to be given more data. Perhaps most distressing is the finding that the average of anterior centra 3-6 is not a good predictor of average shape; this regression (not reported), was not significant, with a p-value of 0.13, even though the two measures are not independent, and

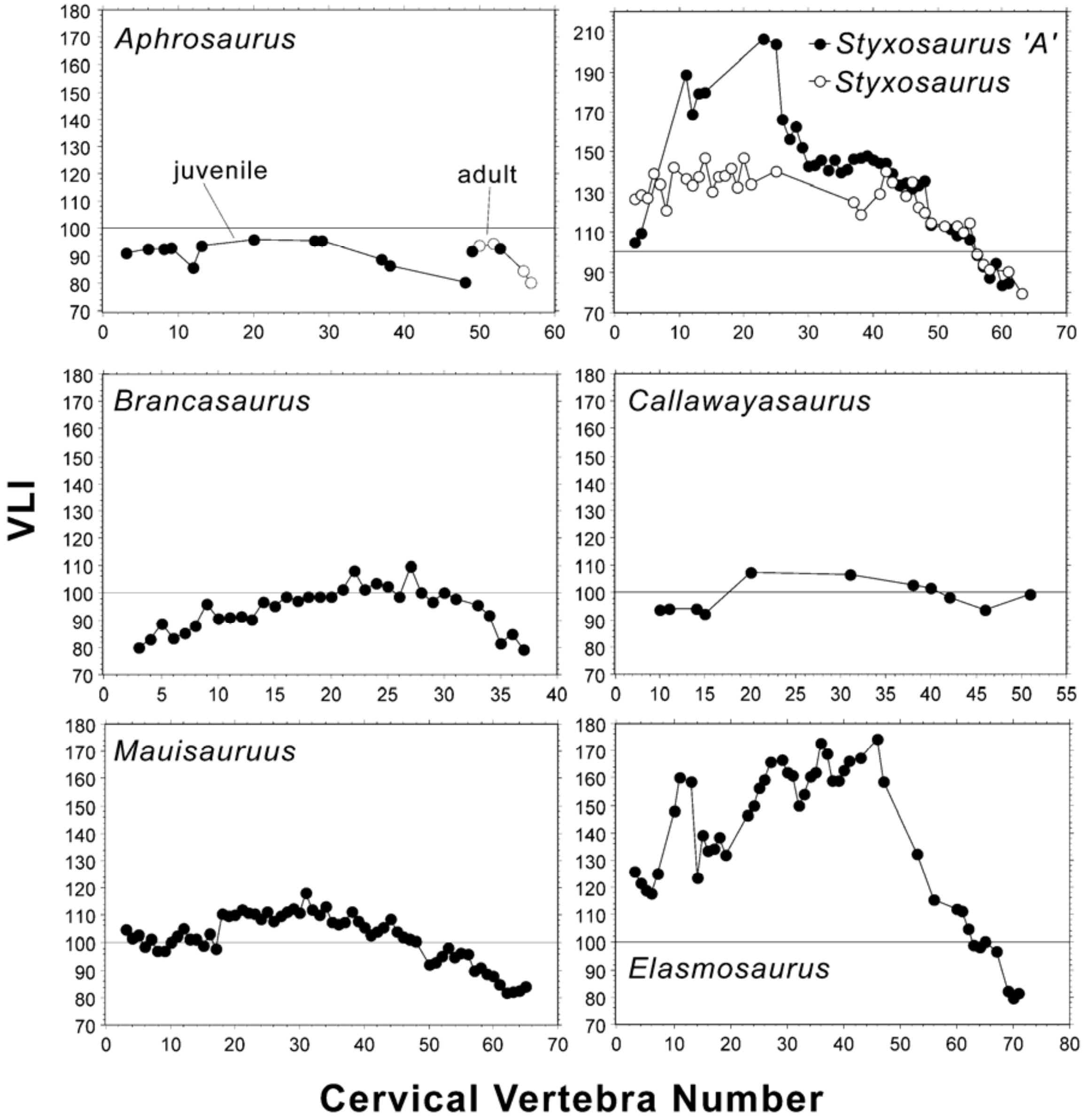

FIGURE 3. Representative VLI shape curves for some elasmosaur taxa. The VLI measure is a shape metric that is very similar to lnPC 2 score, and can be used interchangeably. *Aphrosaurus* is a juvenile with a flat shape curve, but note that it also lacks the last nine cervicals. The adult *Aphrosaurus* centra graphed in this plot are taken from the holotype skeleton; open circles are centra with accurate length measurements, but interpolated face dimensions. *Callawayasaurus* also has a flat shape curve, while *Mauisaurus* is a representative non-elongate elasmosaur. *Elasmosaurus* is elongate, and the overall high VLI and great VLI variability are evident.

spurious significance (Type I statistical error) is actually expected. The C3-C6 average shape is also a poor predictor of the total number of cervicals.

DISCUSSION

Variation is the true hallmark of elasmosaur cervical centra. This generalization is true both within a single column, and among genera. All shape curves in this paper show some variability between adjacent vertebrae in length. This variation is relatively small in *Brancasaurus* and in the more conservative elasmosaurs such as *Mauisaurus*, where the VLI neck curve is fairly smooth, while in *Elasmosaurus* and similar taxa there is tremendous variability from centrum to centrum. In all taxa, the longest vertebrae in the cervical series occur in the middle of the column, although the exact location of maximum length varies considerably. As a generalization, great length in cervical centra also implies great variability in the lengths of those centra, and this is independent of size and other effects.

One factor that is not addressed here is the variability introduced by preservational artifacts, usually compression or distortion of the vertebrae during fossilization. We treated for this by recording measurements for vertebrae that the primary authors felt they could measure accurately. Welles and other authors only included measurements that seemed close to the original values; he would sometimes estimate a measurement, but we always ignored these estimates. Usually Welles would simply not record measures from vertebrae that were too distorted to be useful, and this practice has been continued by other workers. The data set in this study contains measures only from complete, uncompressed centra from which all three dimensions were recorded. However, it would be naive to assume that there is no preservational error in the data set, but we believe this error is small relative to the trends discussed.

In agreement with Welles (1952), we find that at least three sources of variability are important among centra; we summarize our finding about each of these sources below.

Ontogenetic Variation—Ontogenetic variation in elasmosaur centrum dimensions is of large magnitude. There is marked positive allometry among all vertebrae, so that adult centra are relatively longer than those of juveniles by 20 percent or more. Also, the positive allometry in mid-cervical centra is larger than at either end of the neck, so that adult animals have a bowed shape curve (on either lnPC2 score or VLI plots), while juveniles have relatively flat shape curves. These features are elaborations of patterns already present in other plesiosaurs, particularly *Cryptoclidus*, for which good axial columns and growth series are known (Brown 1981, Andrews 1910). Both of these ontogenetic features are present in *Cryptoclidus* but are more pronounced in elasmosaurs. The evidence from the two *Styxosaurus* specimens also demonstrates that the allometric lengthening of mid-cervical centra continues very late into ontogeny. It might also imply that intracolumn centrum variability increases with age, but we do not have the data to test this inference.

Elasmosaurs also have many more vertebrae than more plesiomorphic taxa, and are unique in possessing mid-column centra that are much longer than those at either end. Given that plesiosaurs presumably had indeterminate growth like most reptiles, the use of centrum dimensions in taxonomy therefore seems inadvisable, at least at face value. Centrum dimensions from different parts of the column differ greatly, as do dimensions from the same part of the column over ontogeny. Ontogenetic allometry is also complex, with no simple function describing the relation between size and shape, making taxonomic attributions based on raw centrum dimensions inadvisable. However, it may be possible to treat the differential allometry in the neck as a proxy for age; the juvenile *Aphrosaurus* has a very flat shape curve, while the huge and presumably fully adult *Thalassomedon* has a very exaggerated bow shape (Figures 2, 4), and this is reflected in the coefficient of variation for the VLI measure (Table 3). The flatness of the cervical shape curve may therefore be useful as an independent means of assessing biological age, with flatter curves indicating younger animals. By this criterion, *Hydralmosaurus* might be classified as a juvenile based on its low VLI coefficient of variation. However, this could just be a characteristic of the genus as well, as its body size is larger than that of *Elasmosaurus*, and other osteological correlates indicate that it is an adult. It is often impossible to untangle the factors contributing to centrum shape variation given the data at hand.

Intraspecific Variation—Leaving aside juveniles for taxonomic purposes, the use of individual centra, or small numbers of centra, seems inadvisable as well. The possession of a bowed shape curve means that shape varies significantly over the column, with relatively long centra in the middle of the column. If this pattern was tightly constrained-- i.e. if the shape curves of elasmosaurs always grew in the same way-- one might be able to use data from a few vertebrae to essentially predict the rest of the shape curve. However, such a strategy would rest on tight correlations in shape within different parts of the column. Our analyses show that such tight correlation does not exist; in fact, cervical dimensions prove to be poor predictors of each other. For example, the average VLI of C3-C6 is not tightly correlated to the average VLI of the neck as a whole. Average VLI is not correlated with the number of cervicals, and neither of these measures is correlated with body size. Number of cervicals is also not correlated with shape range, probably because shape range has a very strong ontogenetic component. Lastly, there is no real pattern to elasmosaur neck shape curves beyond a vague statement that mid-cervicals are longer. The position of the longest centra in different necks varies markedly, and *Elasmosaurus* actually has two length peaks rather than one. One does not get the impression of a tightly constrained growth program when looking at elasmosaur neck shape curves; the impression is of a loosely constrained process in which dimensions of individual centra mattered less than the length of the neck as a whole.

Interspecific Variation—Given the large magnitude of ontogenetic and intraspecific variation the outlook for identifying useful interspecific variation seems dim. However, there are some recognizable groupings among elasmosaur taxa. These

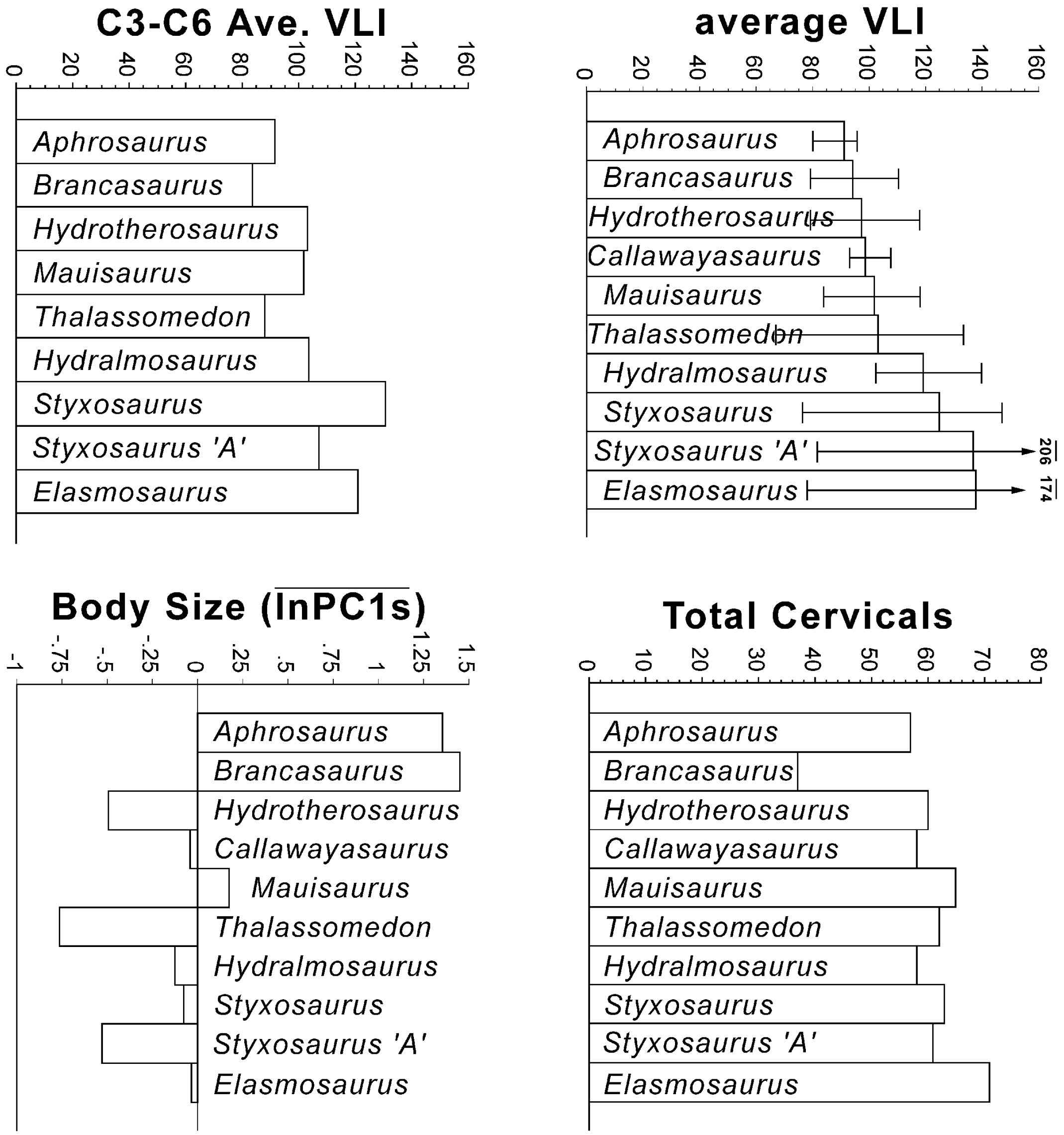

FIGURE 4. Plots of various cervical centrum measures in different elasmosaur taxa. Note that VLI variance tends to increase over ontogeny, as demonstrated by the very low range of VLI in *Aphrosaurus*. The four properties graphed here are poorly correlated; for further discussion see text.

TABLE 3. Summary statistics of the VLI index for eight adult elasmosaurs, one juvenile elasmosaur, and *Brancasaurus*. The statistics for *Callawayasaurus* are approximate given the lack of centra at the ends of the column, and the coefficient of variation for *Aphrosaurus* is probably a slight underestimate.

Taxon	Location	Age	$VLI_{average}$	$VLI_{C3\text{-}C6ave}$	VLI_{min}	VLI_{max}	$VLI_{coeffvar}$
Brancasaurus	Central Europe	Berriasian	94	84	79	110	8.31
Aphrosaurus	California	Camp/Maas	91	92	80	96	5.29
Callawayasaurus	Colombia	Valanginian	99	--	92	107	5.57
Hydrotherosaurus	California	Camp/Maas	97	103	79	118	11.47
Mauisaurus	New Zealand	Camp/Maas	101	102	82	118	8.59
Thalassomedon	WIS	Cenomanian	103	88	68	134	15.95
Hydralmosaurus	WIS	Campanian	118	103	100	140	11.63
Styxosaurus	WIS	Santonian	125	131	79	147	13.36
Styxosaurus 'A'	WIS	Campanian	137	107	84	206	22.32
Elasmosaurus	WIS	Santonian	138	121	80	174	19.72

differences are not extreme, and are probably best characterized as tendencies or rules of thumb rather than marked divisions. Among the adult elasmosaurs, several have a similar VLI range and average to *Brancasaurus* (*Hydrotherosaurus*, *Callawayasaurus*, and *Mauisaurus*, shown in Figures 2, 3; VLI ranges shown in Figure 4 and Table 3). This group of animals have VLI curves that are actually quite similar to that of *Brancasaurus*, being smooth curves spanning about 30 VLI points, and bracketing 100. There is a modest increase in average VLI but it is not marked (less than 10%); these animals increase neck length primarily by adding vertebrae of similar shape, not by making centra longer (see Figure 4 and Table 3).

This group contrasts markedly with a second group, comprised of *Styxosaurus* and *Elasmosaurus*. These animals have VLI ranges of 60 to 100, elevated average VLI (125-138, or 30% or more compared to *Brancasaurus*), and possess some mid-cervical vertebrae that are very long, with lengths 1.5 to 2 times centrum diameter. These taxa also exhibit erratic variation in centrum length, as noted above (e.g. *Elasmosaurus*, Figure 3, Table 3). Lastly, there are two taxa that are intermediate between these two extremes. *Thalassomedon* has a wide range of VLI and a rather large maximum VLI, but an average VLI much nearer the short-centrumed group, while *Hydralmosaurus* has a narrow range of VLI but an average VLI of 118, close to that of the long-centrumed group. Other factors may be at work in these taxa, such as ontogenetic factors in *Hydralmosaurus* as mentioned above, or ontogenetic and/or body size effects in *Thalassomedon*. But this is speculation; we do not have the data at present to test these hypotheses. The two 'groups' described above are really the two ends of a continuum, marked on the one hand by a conservative group of animals that differ from *Brancasaurus* primarily in the addition of vertebrae, and on the other hand by an extreme group characterized by long centra and high centrum variability.

A last variable of taxonomic relevance is the number of cervicals. This character is a traditional one in plesiosaur systematics (O'Keefe 2001b, Brown 1981), although it is usually dealt with rather vaguely (Sato 2002 attempts to gap code this character). The number of cervical vertebrae in elasmosaurs, at least in this study, is actually rather constant. The range for true elasmosaurs in this data set is 57-65, which is quite small given the lengths and numbers of the centra involved. The only exception is *Elasmosaurus*, whose 71 cervicals is the highest number currently known. There is some evidence that *Cryptoclidus* shows intraspecific variation in the number of cervicals, although lack of good collection data precludes certainty (Brown 1981). There is documented intraspecific variation in the number of presacral vertebrae in some pachypleurosaurs (O'Keefe et al. 1999). No elasmosaur taxon is known from enough complete, articulated necks to address this question, but given the possible variation in *Cryptoclidus* , the known variation in nothosaurs, and the relatively chaotic nature of elasmosaur neck segmentation, it would not be surprising at all if intraspecific variation occurred in elasmosaurs as well. Indeed, there is some debate as to the correct number of cervicals in *Styxosaurus*, with Carpenter (1999) counting 62 in both specimens while Welles counted 63 in the smaller and 61 in the larger specimen (Welles 1943; Welles and Bump 1949). As with other neck measures, therefore, small differences in the number of cervicals should not be given excessive taxonomic weight. The only animal that seems truly different is *Elasmosaurus*, with the high total of 71 cervicals. *Elasmosaurus* also has the highest average VLI of all elasmosaurs, but does not have the greatest range of VLI, and is relatively small in terms of body size. Again, variability reigns.

Biogeographic Patterns and Attempted Referrals—Perhaps the most interesting pattern arising from this data set is shown in Figure 5, which plots an average shape variable (taxon average lnPC2score in this case, although average VLI gives the same pattern) against body size. The age and area of discovery for each taxon is recorded in Table 3. Clearly, most of the taxa in the data set are Late Cretaceous in age, but what is remarkable is that all of the extreme group-- called hereafter the 'elongate' group-- were denizens of the Western Interior Seaway (WIS). No animal older than the Santonian shows this extreme morphology, while contemporaneous animals outside the WIS are also not elongate (for instance *Hydrotherosaurus* from California or *Mauisaurus* from New Zealand). So based solely on data from complete necks, we might conclude that elongate cervical morphology-- characterized by very long mid-cervicals and high length variability-- was an endemic feature to elasmosaurs of the WIS of the end Cretaceous. This is an intriguing biogeographic hypothesis, but clearly the sampling of the complete-neck data set is not exhaustive. We know many more elasmosaurs than just those represented by complete necks. We will therefore try to test this biogeographic hypothesis by attempting to classify other incomplete elasmosaur specimens from various parts of the world. Given the analyses performed above, we propose the use of the following rules of thumb:

-- For complete or mostly complete necks sampled evenly, an average VLI of <110 represents a non-elongate animal. The VLI of any single mid-cervical

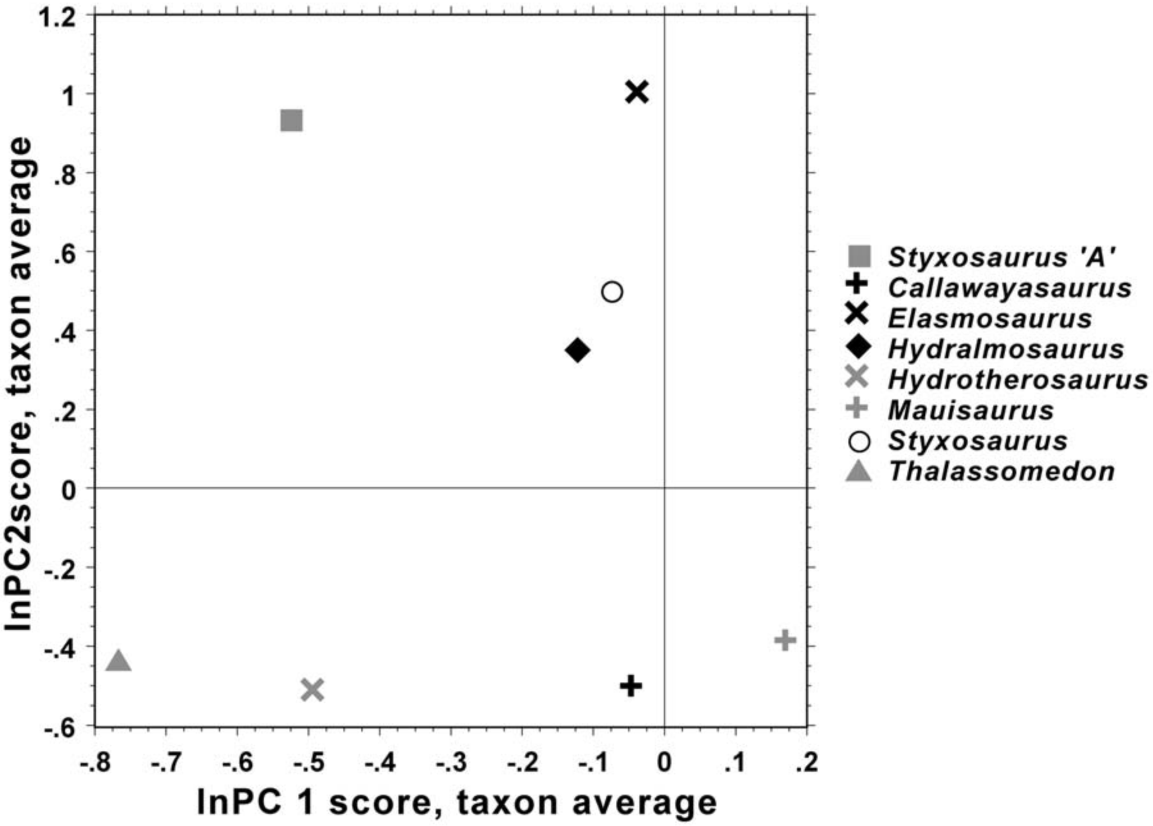

FIGURE 5. Average centrum size (lnPC1 score) and average centrum shape (lnPC2 score) for eight adult elasmosaur genera. Note that large size is to the left of the plot. Latest Cretaceous WIS taxa are indicated. For discussion see text.

vertebra should not range above about 130 for inclusion in this group.

--The lack of one or both ends of a cervical column will result in increased average VLI and decreased VLI range, due to the loss of the shortest centra. However, average VLI for partial necks will never rise above about 120 in non-elongate animals.

-- The VLI of C3-C6 is not a good predictor of the average VLI, as noted above. However, the two taxa with average$\mathrm{VLI}_{\mathrm{C3-C6}}$ >120 are elongate, so that if this number is quite high in a fragmentary anterior neck, it is evidence that the neck was elongate. Note that the reverse is not true-- some elongate taxa have an average $\mathrm{VLI}_{\mathrm{C3-C6}}$ value that is indistinguishable from non-elongate taxa.

-- Possession of mid-cervical centra with a VLI > 135 is usually indicative of an elongate neck.

Note that all of these rules rely on detailed knowledge of the position of the centra in the column; without this knowledge, individual cervical centra dimensions will be almost useless taxonomically except for the special case of very long ones (VLI >150). These rules will classify the elongate and non-elongate taxa in the complete-neck data set correctly, but are equivocal about *Thalassomedon* and *Hydralmosaurus*. *Thalassomedon* has an average VLI of 103 and so should be non-elongate, but has a maximum VLI of 134. *Hydralmosaurus* has an average VLI of 118, higher than non-elongate taxa but not high enough to qualify as elongate, although its maximum VLI is 140. Other factors may be at work here, but the conservative course is to not attempt to classify either of these taxa into the elongate or non-elongate categories.

Table 4 contains summary information for partial cervical series of various taxa collected from the literature, along with suggested classifications where possible. Obviously, specimens with more complete necks are easier to classify; therefore, the holotype of *Terminonatator ponteixensis* Sato 2003 contains the anterior half of the neck and is clearly an elongate taxon, possessing an average VLI of 126 and a maximum preserved VLI of 135. We might expect

TABLE 4. Attempted classifications of partial cervical series. Citations for each specimen are, in order: Sato 2003, Welles 1949, Wiffen and Moiseley 1986, Persson 1982, Welles and Gregg 1971, Sato et al. 2006.

Specimen	Taxon	Location	Age	Vertebrae Preserved	VLI_{avg}	Suggested Classification
RSMP2414.1	*Terminonatator ponteixensis*	Saskatchewan	Campanian	27 anterior	126	Elongate
SMUSMP 69120	*Libonectes morgani*	Texas	Coniacian	13, mid-cervical	108	Not elongate
NZGS CD426	*Tuarangisaurus keyesi*	New Zealand	Camp/Maas	C3-C8	114	unknown
QM F11050, QM F12216,-17	*Eromangasaurus carinognathus*	Queensland, Australia	Upper Albian	3 anterior cervicals	105	unknown
NZCS CD443	unknown	New Zealand	Camp/Maas	6 posterior cervicals; one mid-cervical	85, 113	Not elongate; *Mauisaurus*
NSM PV15025	*Futabasaurus suzukii*	Japan	Santonian	13 posterior cervicals	75.3	Not elongate

more posterior centra in this taxon to be even longer. This fourth elongate taxon fits with the biogeographic pattern mentioned above, as *Terminonatator* is a WIS taxon and is latest Cretaceous in age. The second taxon classified is *Libonectes morgani*, and it is clearly not elongate, with a mid-cervical average VLI of 108. *Libonectes* is also a WIS taxon, and proves that more conservative, non-elongate taxa were still present there in the Late Cretaceous, at least in Texas in the Coniacian.

Two other austral elasmosaurs are of central importance for testing the above biogeographic pattern: *Eromangasaurus carinognathus* Kear 2005 and *Tuarangisaurus keyesi* Wiffen and Moiseley 1986. The holotype of *Eromangasaurus* preserves just three anterior centra, whose average VLI is 105. Numbers in this range are shared by both elongate and non-elongate taxa, so no classification is possible for this genus. The situation with *Tuarangisaurus* is more complex. Vertebrae C3-C8 are preserved with the holotype skull, and the average VLI for these is 114. This is quite high for a series of anterior cervicals, but actually has no analog among the specimens in the complete neck data set. Some elongate taxa have $VLI_{C3\text{-}C6}$ averages about 10% shorter than this, while other elongate taxa are about 10% longer than this. There is no non-elongate taxa with a $VLI_{C3\text{-}C6}$ average this high, and this includes *Thalassomedon*. There is therefore some evidence that *Tuarangisaurus* may be an elongate taxon. If this is true, *Tuarangisaurus* would be the only elongate taxon known outside of the WIS. However, given the known variability in elasmosaur necks, we are uncomfortable about making this assignment without more cervical material. It is entirely possible that *Tuarangisaurus* does not follow either of the patterns outlined above; it could be more like *Hydralmosaurus*, or it could have another pattern entirely. More and better cervical material could solve this mystery. Lastly, the recently described *Futabasaurus* (Sato et al. 2006) from the Santonian of Japan is clearly not elongate, having 13 posterior cervicals with an average VLI of only 75.3.

CONCLUSIONS

The main finding of this study is the high degree of variability in the length of elasmosaur cervical centra. This variability arises from at least three sources: ontogenetic allometry, intracolumn variation, and taxonomic variation. While we might wish for more and better ontogenetic data, we infer that ontogenetic allometry in cervical centra is significant and complex, with all vertebrae becoming appreciably longer with growth, and the mid-cervicals outstripping those at either end. Intracolumn variation is also significant, being a minor factor in non-elongate taxa, and a pronounced feature of elongate taxa. This fact is very relevant for assigning centra to different taxa; given that VLI can vary between 20 and 40 percent in a single column, one must know the location of the centrum in the column-- at least to region-- for a taxonomically meaningful comparison to be made.

Lastly, taxonomic variation is also present but is often confounded with the first two sources of variation. That being said, there are two tendencies discernable in the data, a group of conservative taxa termed non-elongate that lack very long centra, and a group of elongate taxa that possess very long centra in the mid-cervical region. Interestingly, the number of cervical vertebrae is not correlated with the length of cervical centra, and is actually rather constant except for *Elasmosaurus*. All presently known elongate taxa occur in the Late Cretaceous WIS, with the possible exception of *Tuarangisaurus*. However, much more research is certainly needed on this question, as sampling in this study is not exhaustive. We furnish a set of rules of thumb that might be used to distinguish between elongate and non-elongate taxa given partial cervical material. We stress that these are not hard-and-fast rules, however, and that the overarching fact of elasmosaur cervical variability -- ontogenetic, intrataxic, and intertaxic-- must always be kept in mind.

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APPENDIX

Data set used for the core analyses in this paper. The specimen number for *Brancasaurus brancai* is currently unavailable. Variables are: L, length; B, breadth; H, height; GM, geometric mean; VLI, vertebral length index; lnPC1, principal component 1 score, lnPC2, principal component 2 score. All measurements in mm. Column positions for *Leurospondylus* are conjectural.

Taxon	**Spec. #**	**Position**	**L**	**H**	**B**	**GM**	**VLI**	**lnPC1**	**lnPC2**
Callawayasaurus	UCMP 38349	10	38	32	49	38.92	93.8	1.106	-0.739
Callawayasaurus	UCMP 38349	11	40	34	51	40.93	94.1	0.996	-0.724
Callawayasaurus	UCMP 38349	14	46	42	56	47.47	93.9	0.676	-0.698
Callawayasaurus	UCMP 38349	15	47	45	57	49.21	92.2	0.598	-0.759
Callawayasaurus	UCMP 38349	20	65	50	71	61.08	107.4	0.128	-0.137
Callawayasaurus	UCMP 38349	31	82	67	87	77.85	106.5	-0.399	-0.167
Callawayasaurus	UCMP 38349	38	88	76	95	85.59	102.9	-0.606	-0.319
Callawayasaurus	UCMP 38349	40	89	79	96	87.33	101.7	-0.65	-0.359
Callawayasaurus	UCMP 38349	42	88	82	97	88.39	98.3	-0.676	-0.502
Callawayasaurus	UCMP 38349	46	88	88	100	91.42	93.6	-0.75	-0.709
Callawayasaurus	UCMP 38349	51	99	92	107	98.69	99.5	-0.916	-0.451
Leurospondylus	AMNH 5261	45	22	17	31	22.56	91.7	2.291	-0.819
Leurospondylus	AMNH 5261	54	25	22	40	27.93	80.6	1.822	-1.459
Leurospondylus	AMNH 5261	55	26	23	41	28.95	81.3	1.744	-1.425
Leurospondylus	AMNH 5261	56	27	23	42	29.56	83.1	1.699	-1.329
Leurospondylus	AMNH 5261	57	27	25	42	30.39	80.6	1.639	-1.453
Leurospondylus	AMNH 5261	58	27	24	41	29.74	83.1	1.687	-1.312
Leurospondylus	AMNH 5261	59	27	24	42	29.98	81.8	1.668	-1.392
Leurospondylus	AMNH 5261	60	27	25	43	30.63	79.4	1.621	-1.532
Leurospondylus	AMNH 5261	61	26	28	42	31.16	74.3	1.585	-1.798
Leurospondylus	AMNH 5261	62	26	28	44	31.65	72.2	1.549	-1.954
Styxosaurus	AMNH 5835	3	40	22	41	32.93	127.0	1.474	0.655
Styxosaurus	AMNH 5835	4	40	22	40	32.66	129.0	1.493	0.738
Styxosaurus	AMNH 5835	5	44	29	40	36.96	127.5	1.23	0.773
Styxosaurus	AMNH 5835	6	46	30	36	36.63	139.4	1.256	1.284
Styxosaurus	AMNH 5835	7	47	30	40	38.21	134.3	1.16	1.031
Styxosaurus	AMNH 5835	8	46	33	43	40.12	121.1	1.051	0.546
Styxosaurus	AMNH 5835	9	52	30	43	40.48	142.5	1.033	1.261
Styxosaurus	AMNH 5835	11	56	33	49	44.73	136.6	0.813	1.028
Styxosaurus	AMNH 5835	12	56	32	52	45.16	133.3	0.789	0.874
Styxosaurus	AMNH 5835	13	60	35	52	47.61	137.9	0.677	1.064
Styxosaurus	AMNH 5835	14	64	35	52	48.65	147.1	0.632	1.365
Styxosaurus	AMNH 5835	15	62	39	56	51.15	130.5	0.52	0.807
Styxosaurus	AMNH 5835	16	62	37	53	49.35	137.8	0.6	1.07
Styxosaurus	AMNH 5835	17	67	38	59	52.95	138.1	0.444	1.034
Styxosaurus	AMNH 5835	18	66	36	57	51.15	141.9	0.52	1.159
Styxosaurus	AMNH 5835	19	67	40	61	54.46	132.7	0.382	0.846
Styxosaurus	AMNH 5835	20	75	40	62	56.85	147.1	0.291	1.318
Styxosaurus	AMNH 5835	21	69	36	67	54.79	134.0	0.365	0.825

Taxon	**Spec. #**	**Position**	**L**	**H**	**B**	**GM**	**VLI**	**lnPC1**	**lnPC2**
Styxosaurus	AMNH 5835	25	80	50	64	63.23	140.4	0.063	1.182
Styxosaurus	AMNH 5835	37	95	62	90	80.58	125.0	-0.473	0.523
Styxosaurus	AMNH 5835	38	95	60	100	82.55	118.8	-0.531	0.218
Styxosaurus	AMNH 5835	41	110	70	100	91.24	129.4	-0.743	0.674
Styxosaurus	AMNH 5835	42	110	65	92	86.58	140.1	-0.626	1.064
Styxosaurus	AMNH 5835	43	110	66	97	88.57	135.0	-0.678	0.864
Styxosaurus	AMNH 5835	45	115	72	107	95.61	128.5	-0.846	0.613
Styxosaurus	AMNH 5835	46	118	70	105	94.93	134.9	-0.83	0.839
Styxosaurus	AMNH 5835	47	112	72	111	95.93	122.4	-0.856	0.367
Styxosaurus	AMNH 5835	48	110	76	107	95.91	120.2	-0.854	0.325
Styxosaurus	AMNH 5835	49	118	86	120	106.29	114.6	-1.079	0.085
Styxosaurus	AMNH 5835	51	115	80	123	103.72	113.3	-1.028	-0.011
Styxosaurus	AMNH 5835	53	116	85	120	105.28	113.2	-1.059	0.023
Styxosaurus	AMNH 5835	54	115	86	123	106.25	110.0	-1.08	-0.118
Styxosaurus	AMNH 5835	55	120	85	124	107.64	114.8	-1.108	0.071
Styxosaurus	AMNH 5835	56	114	95	135	112.96	99.1	-1.216	-0.619
Styxosaurus	AMNH 5835	57	109	90	142	111.16	94.0	-1.185	-0.918
Styxosaurus	AMNH 5835	58	105	95	135	109.91	91.3	-1.159	-1.003
Styxosaurus	AMNH 5835	61	105	93	140	110.46	90.1	-1.172	-1.094
Styxosaurus	AMNH 5835	63	96	97	145	110.01	79.3	-1.166	-1.693
Hydralmosaurus	AMNH 1495	3	41	33	45	39.20	105.1	1.097	-0.144
Hydralmosaurus	AMNH 1495	4	42	34	46	40.20	105.0	1.042	-0.15
Hydralmosaurus	AMNH 1495	5	44	34	50	41.98	104.8	0.945	-0.212
Hydralmosaurus	AMNH 1495	6	43	36	50	42.46	100.0	0.92	-0.404
Hydralmosaurus	AMNH 1495	7	47	35	50	43.33	110.6	0.878	0.053
Hydralmosaurus	AMNH 1495	8	52	37	51	45.95	118.2	0.753	0.377
Hydralmosaurus	AMNH 1495	10	53	40	49	46.83	119.1	0.715	0.484
Hydralmosaurus	AMNH 1495	11	54	40	55	48.97	113.7	0.613	0.184
Hydralmosaurus	AMNH 1495	13	56	41	57	50.57	114.3	0.542	0.198
Hydralmosaurus	AMNH 1495	14	65	45	60	55.76	123.8	0.332	0.584
Hydralmosaurus	AMNH 1495	15	68	44	62	56.80	128.3	0.292	0.719
Hydralmosaurus	AMNH 1495	16	71	48	60	58.67	131.5	0.225	0.901
Hydralmosaurus	AMNH 1495	17	72	50	62	60.41	128.6	0.161	0.796
Hydralmosaurus	AMNH 1495	19	78	54	64	64.33	132.2	0.025	0.949
Hydralmosaurus	AMNH 1495	22	85	57	68	68.77	136.0	-0.12	1.068
Hydralmosaurus	AMNH 1495	23	87	57	69	69.65	138.1	-0.147	1.127
Hydralmosaurus	AMNH 1495	24	90	61	72	73.08	135.3	-0.252	1.042
Hydralmosaurus	AMNH 1495	26	95	61	76	75.75	138.7	-0.331	1.114
Hydralmosaurus	AMNH 1495	27	95	64	77	77.31	134.8	-0.376	0.999
Hydralmosaurus	AMNH 1495	28	98	64	76	77.78	140.0	-0.387	1.188
Hydralmosaurus	AMNH 1495	29	99	66	78	79.53	137.5	-0.436	1.102
Hydralmosaurus	AMNH 1495	30	98	79	81	85.21	122.5	-0.586	0.661
Hydralmosaurus	AMNH 1495	31	101	72	83	84.14	130.3	-0.56	0.858
Hydralmosaurus	AMNH 1495	32	98	74	84	84.40	124.1	-0.568	0.636
Hydralmosaurus	AMNH 1495	34	94	75	99	88.31	108.0	-0.675	-0.129
Hydralmosaurus	AMNH 1495	42	120	81	141	110.56	108.1	-1.172	-0.288

Taxon	**Spec. #**	**Position**	**L**	**H**	**B**	**GM**	**VLI**	**lnPC1**	**lnPC2**
Hydralmosaurus	AMNH 1495	47	113	86	124	105.92	107.6	-1.074	-0.227
Hydralmosaurus	AMNH 1495	50	113	89	127	107.99	104.6	-1.117	-0.358
Hydralmosaurus	AMNH 1495	51	111	90	125	107.18	103.3	-1.1	-0.405
Hydralmosaurus	AMNH 1495	53	115	95	134	113.01	100.4	-1.217	-0.553
Hydralmosaurus	AMNH 1495	55	114	99	125	111.63	101.8	-1.187	-0.422
Hydralmosaurus	AMNH 1495	56	110	94	126	108.71	100.0	-1.131	-0.539
Elasmosaurus	ANSP 18001	3	39	25	37	32.93	125.8	1.48	0.691
Elasmosaurus	ANSP 18001	4	42	27	42	36.12	121.7	1.276	0.498
Elasmosaurus	ANSP 18001	5	41	31	38	36.29	118.8	1.271	0.516
Elasmosaurus	ANSP 18001	6	43	30	43	38.00	117.8	1.166	0.373
Elasmosaurus	ANSP 18001	7	45	27	45	37.82	125.0	1.174	0.589
Elasmosaurus	ANSP 18001	10	51	27	42	38.53	147.8	1.14	1.406
Elasmosaurus	ANSP 18001	11	56	30	40	40.51	160.0	1.037	1.85
Elasmosaurus	ANSP 18001	13	61	30	47	43.97	158.4	0.853	1.709
Elasmosaurus	ANSP 18001	14	55	35	54	46.84	123.6	0.709	0.53
Elasmosaurus	ANSP 18001	15	57	32	50	44.84	139.0	0.807	1.088
Elasmosaurus	ANSP 18001	16	58	35	52	47.08	133.3	0.701	0.905
Elasmosaurus	ANSP 18001	17	61	36	55	49.24	134.1	0.603	0.911
Elasmosaurus	ANSP 18001	18	65	36	58	51.19	138.3	0.517	1.03
Elasmosaurus	ANSP 18001	19	66	40	60	53.89	132.0	0.406	0.831
Elasmosaurus	ANSP 18001	23	71	41	56	54.41	146.4	0.39	1.367
Elasmosaurus	ANSP 18001	24	75	43	57	56.63	150.0	0.304	1.493
Elasmosaurus	ANSP 18001	25	79	45	56	58.15	156.4	0.249	1.728
Elasmosaurus	ANSP 18001	26	82	47	56	59.74	159.2	0.192	1.837
Elasmosaurus	ANSP 18001	27	83	46	54	58.84	166.0	0.227	2.048
Elasmosaurus	ANSP 18001	29	90	50	58	63.64	166.7	0.056	2.063
Elasmosaurus	ANSP 18001	30	90	50	61	64.72	162.2	0.017	1.894
Elasmosaurus	ANSP 18001	31	90	52	60	65.21	160.7	0.002	1.891
Elasmosaurus	ANSP 18001	32	93	60	64	70.65	150.0	-0.173	1.615
Elasmosaurus	ANSP 18001	33	94	55	67	69.93	154.1	-0.153	1.641
Elasmosaurus	ANSP 18001	34	98	60	62	71.13	160.7	-0.185	1.966
Elasmosaurus	ANSP 18001	35	98	61	60	70.75	162.0	-0.171	2.052
Elasmosaurus	ANSP 18001	36	102	56	62	70.45	172.9	-0.164	2.256
Elasmosaurus	ANSP 18001	37	104	59	64	72.92	169.1	-0.239	2.163
Elasmosaurus	ANSP 18001	38	105	62	70	76.62	159.1	-0.35	1.833
Elasmosaurus	ANSP 18001	39	105	64	68	76.69	159.1	-0.35	1.883
Elasmosaurus	ANSP 18001	40	110	69	66	79.07	163.0	-0.413	2.089
Elasmosaurus	ANSP 18001	41	108	68	62	76.60	166.2	-0.342	2.235
Elasmosaurus	ANSP 18001	43	113	67	68	79.80	167.4	-0.434	2.158
Elasmosaurus	ANSP 18001	46	115	65	67	79.07	174.2	-0.413	2.335
Elasmosaurus	ANSP 18001	47	115	70	75	84.14	158.6	-0.553	1.847
Elasmosaurus	ANSP 18001	53	115	82	92	94.94	132.2	-0.823	0.927
Elasmosaurus	ANSP 18001	56	112	84	110	100.68	115.5	-0.959	0.168
Elasmosaurus	ANSP 18001	60	112	90	110	103.02	112.0	-1.008	0.065
Elasmosaurus	ANSP 18001	61	110	90	108	101.78	111.1	-0.981	0.043
Elasmosaurus	ANSP 18001	62	110	95	115	105.82	104.8	-1.068	-0.248

Taxon	**Spec. #**	**Position**	**L**	**H**	**B**	**GM**	**VLI**	**lnPC1**	**lnPC2**
Elasmosaurus	ANSP 18001	63	105	92	120	104.56	99.1	-1.045	-0.561
Elasmosaurus	ANSP 18001	64	103	95	115	103.53	98.1	-1.022	-0.556
Elasmosaurus	ANSP 18001	65	105	85	125	103.23	100.0	-1.02	-0.58
Elasmosaurus	ANSP 18001	67	110	96	131	110.90	96.9	-1.176	-0.701
Elasmosaurus	ANSP 18001	69	96	98	135	107.79	82.4	-1.118	-1.468
Elasmosaurus	ANSP 18001	70	92	97	134	105.65	79.7	-1.076	-1.627
Elasmosaurus	ANSP 18001	71	92	95	131	104.13	81.4	-1.043	-1.52
Aphrosaurus	CIT 2832	3	20	18	26	21.01	90.9	2.452	-0.76
Aphrosaurus	CIT 2832	6	25	21	33	25.79	92.6	2.003	-0.745
Aphrosaurus	CIT 2832	8	25	18	36	25.22	92.6	2.046	-0.808
Aphrosaurus	CIT 2832	9	26	19	37	26.26	92.9	1.959	-0.797
Aphrosaurus	CIT 2832	12	27	22	41	28.89	85.7	1.749	-1.182
Aphrosaurus	CIT 2832	13	30	22	42	30.16	93.8	1.657	-0.771
Aphrosaurus	CIT 2832	20	37	26	51	36.48	96.1	1.242	-0.69
Aphrosaurus	CIT 2832	28	43	32	58	42.89	95.6	0.89	-0.727
Aphrosaurus	CIT 2832	29	45	33	61	44.74	95.7	0.798	-0.729
Aphrosaurus	CIT 2832	37	48	39	69	50.35	88.9	0.539	-1.089
Aphrosaurus	CIT 2832	38	47	40	69	50.42	86.2	0.535	-1.225
Aphrosaurus	CIT 2832	48	49	45	77	55.15	80.3	0.338	-1.573
Thalassomedon	CMNH 1588	3	38	44	41	40.78	89.4	1.017	-0.615
Thalassomedon	CMNH 1588	4	47	50	55	50.36	89.5	0.551	-0.796
Thalassomedon	CMNH 1589	5	44	43	55	46.85	89.8	0.704	-0.88
Thalassomedon	CMNH 1590	6	47	45	67	51.93	83.9	0.474	-1.301
Thalassomedon	CMNH 1588	7	54	39	60	49.98	109.1	0.564	-0.07
Thalassomedon	CMNH 1588	8	46	46	70	52.70	79.3	0.44	-1.581
Thalassomedon	CMNH 1588	9	54	46	67	54.79	95.6	0.361	-0.685
Thalassomedon	CMNH 1588	10	56	50	68	57.30	94.9	0.265	-0.689
Thalassomedon	CMNH 1588	11	54	50	67	56.33	92.3	0.302	-0.809
Thalassomedon	CMNH 1588	12	57	54	63	57.65	97.4	0.257	-0.464
Thalassomedon	CMNH 1588	13	58	52	67	58.44	97.5	0.224	-0.533
Thalassomedon	CMNH 1588	14	57	54	74	60.82	89.1	0.133	-1.004
Thalassomedon	CMNH 1588	15	65	56	75	64.60	99.2	0.005	-0.489
Thalassomedon	CMNH 1588	16	62	58	79	65.46	90.5	-0.027	-0.936
Thalassomedon	CMNH 1588	17	63	59	83	67.29	88.7	-0.088	-1.052
Thalassomedon	CMNH 1588	18	72	67	82	73.09	96.6	-0.263	-0.576
Thalassomedon	CMNH 1588	19	80	62	80	73.17	112.7	-0.262	0.114
Thalassomedon	CMNH 1588	20	79	63	82	73.86	109.0	-0.284	-0.051
Thalassomedon	CMNH 1588	21	87	66	85	78.39	115.2	-0.412	0.21
Thalassomedon	CMNH 1588	22	87	79	87	83.87	104.8	-0.558	-0.135
Thalassomedon	CMNH 1588	23	97	72	86	84.00	122.8	-0.559	0.55
Thalassomedon	CMNH 1588	24	97	73	87	84.71	121.3	-0.578	0.491
Thalassomedon	CMNH 1588	25	90	77	90	85.06	107.8	-0.59	-0.052
Thalassomedon	CMNH 1588	26	95	74	84	83.53	120.3	-0.546	0.491
Thalassomedon	CMNH 1588	27	103	73	83	85.08	132.1	-0.584	0.929
Thalassomedon	CMNH 1588	28	105	73	100	91.11	121.4	-0.74	0.394

Taxon	Spec. #	Position	L	H	B	GM	VLI	lnPC1	lnPC2
Thalassomedon	CMNH 1588	29	104	79	95	91.66	119.5	-0.75	0.404
Thalassomedon	CMNH 1588	30	105	83	93	92.81	119.3	-0.776	0.447
Thalassomedon	CMNH 1588	32	110	95	90	97.53	118.9	-0.879	0.574
Thalassomedon	CMNH 1588	33	115	82	97	96.63	128.5	-0.863	0.749
Thalassomedon	CMNH 1588	34	117	85	103	100.34	124.5	-0.947	0.575
Thalassomedon	CMNH 1588	35	123	81	102	100.08	134.4	-0.94	0.913
Thalassomedon	CMNH 1588	36	118	88	102	101.46	124.2	-0.97	0.596
Thalassomedon	CMNH 1588	37	122	85	109	103.69	125.8	-1.02	0.581
Thalassomedon	CMNH 1588	38	125	97	113	110.55	119.0	-1.159	0.377
Thalassomedon	CMNH 1588	39	123	105	112	112.56	113.4	-1.197	0.214
Thalassomedon	CMNH 1588	40	122	102	110	110.51	115.1	-1.157	0.279
Thalassomedon	CMNH 1588	41	137	105	134	123.85	114.6	-1.41	0.116
Thalassomedon	CMNH 1588	42	127	110	137	123.56	102.8	-1.408	-0.381
Thalassomedon	CMNH 1588	43	132	112	143	127.72	103.5	-1.48	-0.371
Thalassomedon	CMNH 1588	44	129	111	142	126.08	102.0	-1.452	-0.442
Thalassomedon	CMNH 1588	45	134	114	142	128.82	104.7	-1.498	-0.304
Thalassomedon	CMNH 1588	46	131	116	145	129.49	100.4	-1.511	-0.506
Thalassomedon	CMNH 1588	47	137	117	151	133.61	102.2	-1.579	-0.445
Thalassomedon	CMNH 1588	48	140	127	155	139.51	99.3	-1.673	-0.553
Thalassomedon	CMNH 1588	49	135	119	163	137.16	95.7	-1.64	-0.795
Thalassomedon	CMNH 1588	50	130	127	160	137.56	90.6	-1.646	-1.006
Thalassomedon	CMNH 1588	52	120	117	172	133.51	83.0	-1.587	-1.501
Thalassomedon	CMNH 1588	53	130	124	165	137.87	90.0	-1.652	-1.074
Thalassomedon	CMNH 1588	54	140	124	167	141.88	96.2	-1.713	-0.768
Thalassomedon	CMNH 1588	55	136	119	165	138.05	95.8	-1.654	-0.802
Thalassomedon	CMNH 1588	56	130	128	183	144.22	83.6	-1.755	-1.468
Thalassomedon	CMNH 1588	57	136	126	180	144.84	88.9	-1.762	-1.178
Thalassomedon	CMNH 1588	58	123	127	170	137.80	82.8	-1.654	-1.468
Thalassomedon	CMNH 1588	59	115	130	170	135.80	76.7	-1.623	-1.817
Thalassomedon	CMNH 1588	60	113	125	185	137.06	72.9	-1.648	-2.124
Thalassomedon	CMNH 1588	61	110	123	188	135.84	70.7	-1.63	-2.28
Thalassomedon	CMNH 1588	62	110	130	192	139.34	68.3	-1.686	-2.433
Hydrotherosaurus	UCMP 33912	4	37	33	46	38.16	93.7	1.152	-0.698
Hydrotherosaurus	UCMP 33912	5	39	33	38	36.44	109.9	1.262	0.189
Hydrotherosaurus	UCMP 33912	6	42	35	44	39.99	106.3	1.055	-0.044
Hydrotherosaurus	UCMP 33912	12	50	35	56	45.93	109.9	0.748	-0.037
Hydrotherosaurus	UCMP 33912	13	53	38	55	47.84	114.0	0.662	0.173
Hydrotherosaurus	UCMP 33912	15	58	48	60	54.85	107.4	0.366	-0.044
Hydrotherosaurus	UCMP 33912	23	73	50	74	64.37	117.7	0.015	0.267
Hydrotherosaurus	UCMP 33912	32	87	81	86	84.25	104.2	-0.567	-0.133
Hydrotherosaurus	UCMP 33912	33	87	88	95	89.53	95.1	-0.703	-0.59
Hydrotherosaurus	UCMP 33912	34	87	79	90	84.83	103.0	-0.584	-0.249
Hydrotherosaurus	UCMP 33912	35	88	79	80	81.88	110.7	-0.501	0.2
Hydrotherosaurus	UCMP 33912	36	86	82	89	85.24	100.6	-0.594	-0.321
Hydrotherosaurus	UCMP 33912	37	87	82	94	87.14	98.9	-0.644	-0.45
Hydrotherosaurus	UCMP 33912	38	90	83	92	87.85	102.9	-0.66	-0.237

Taxon	**Spec. #**	**Position**	**L**	**H**	**B**	**GM**	**VLI**	**lnPC1**	**lnPC2**
Hydrotherosaurus	UCMP 33912	39	91	87	96	90.85	99.5	-0.734	-0.398
Hydrotherosaurus	UCMP 33912	40	92	86	90	88.90	104.5	-0.684	-0.114
Hydrotherosaurus	UCMP 33912	41	89	86	87	86.94	102.9	-0.634	-0.155
Hydrotherosaurus	UCMP 33912	42	95	88	76	85.59	115.9	-0.592	0.569
Hydrotherosaurus	UCMP 33912	43	94	89	92	91.23	103.9	-0.74	-0.138
Hydrotherosaurus	UCMP 33912	44	91	94	101	94.81	93.3	-0.828	-0.684
Hydrotherosaurus	UCMP 33912	45	93	91	93	91.91	101.1	-0.757	-0.257
Hydrotherosaurus	UCMP 33912	46	95	92	101	95.49	98.4	-0.843	-0.451
Hydrotherosaurus	UCMP 33912	47	94	93	103	96.12	95.9	-0.858	-0.582
Hydrotherosaurus	UCMP 33912	48	90	96	91	91.88	96.3	-0.755	-0.417
Hydrotherosaurus	UCMP 33912	49	89	94	110	96.82	87.3	-0.878	-1.074
Hydrotherosaurus	UCMP 33912	50	88	96	108	96.55	86.3	-0.871	-1.096
Hydrotherosaurus	UCMP 33912	51	96	93	95	94.23	102.1	-0.811	-0.212
Hydrotherosaurus	UCMP 33912	52	87	99	104	95.96	85.7	-0.856	-1.069
Hydrotherosaurus	UCMP 33912	53	99	99	108	101.44	95.7	-0.975	-0.591
Hydrotherosaurus	UCMP 33912	54	89	102	119	102.13	80.5	-0.997	-1.459
Hydrotherosaurus	UCMP 33912	55	86	105	114	100.51	78.5	-0.96	-1.518
Hydrotherosaurus	UCMP 33912	56	91	106	116	103.34	82.0	-1.02	-1.326
Hydrotherosaurus	UCMP 33912	57	91	103	118	102.94	82.4	-1.013	-1.341
Hydrotherosaurus	UCMP 33912	58	88	103	117	101.51	80.0	-0.983	-1.469
Hydrotherosaurus	UCMP 33912	59	87	102	116	100.51	79.8	-0.961	-1.479
Hydrotherosaurus	UCMP 33912	60	88	107	110	100.71	81.1	-0.963	-1.319
Styxosaurus 'A'	SDSM 451	3	33	27	36	31.66	104.8	1.563	-0.112
Styxosaurus 'A'	SDSM 451	4	40	28	45	36.81	109.6	1.231	-0.016
Styxosaurus 'A'	SDSM 451	11	68	31	41	44.05	188.9	0.859	2.626
Styxosaurus 'A'	SDSM 451	12	71	34	50	49.23	169.0	0.61	2.025
Styxosaurus 'A'	SDSM 451	13	78	36	51	52.11	179.3	0.489	2.313
Styxosaurus 'A'	SDSM 451	14	80	40	49	53.71	179.8	0.427	2.409
Styxosaurus 'A'	SDSM 451	23	98	40	55	59.72	206.3	0.196	2.971
Styxosaurus 'A'	SDSM 451	25	106	50	54	65.63	203.8	-0.003	3.067
Styxosaurus 'A'	SDSM 451	26	103	58	66	73.01	166.1	-0.243	2.04
Styxosaurus 'A'	SDSM 451	27	104	61	72	76.68	156.4	-0.353	1.718
Styxosaurus 'A'	SDSM 451	28	110	60	75	78.76	163.0	-0.412	1.868
Styxosaurus 'A'	SDSM 451	29	109	63	80	81.54	152.4	-0.49	1.536
Styxosaurus 'A'	SDSM 451	30	108	66	85	84.24	143.0	-0.563	1.221
Styxosaurus 'A'	SDSM 451	31	111	69	86	86.62	143.2	-0.623	1.244
Styxosaurus 'A'	SDSM 451	32	111	68	84	85.53	146.1	-0.595	1.344
Styxosaurus 'A'	SDSM 451	33	110	72	84	86.91	141.0	-0.629	1.217
Styxosaurus 'A'	SDSM 451	34	111	71	81	85.72	146.1	-0.597	1.402
Styxosaurus 'A'	SDSM 451	35	111	70	89	88.04	139.6	-0.66	1.107
Styxosaurus 'A'	SDSM 451	36	113	75	85	89.24	141.3	-0.686	1.243
Styxosaurus 'A'	SDSM 451	37	115	73	84	88.61	146.5	-0.67	1.404
Styxosaurus 'A'	SDSM 451	38	117	74	85	89.88	147.2	-0.701	1.425
Styxosaurus 'A'	SDSM 451	39	120	76	86	91.80	148.1	-0.746	1.465
Styxosaurus 'A'	SDSM 451	40	121	80	86	93.64	145.8	-0.789	1.427
Styxosaurus 'A'	SDSM 451	41	119	84	81	92.78	144.2	-0.766	1.478

Taxon	**Spec. #**	**Position**	**L**	**H**	**B**	**GM**	**VLI**	**lnPC1**	**lnPC2**
Styxosaurus 'A'	SDSM 451	42	120	82	84	93.42	144.6	-0.782	1.431
Styxosaurus 'A'	SDSM 451	43	119	84	87	95.02	139.2	-0.821	1.238
Styxosaurus 'A'	SDSM 451	44	116	85	89	95.30	133.3	-0.829	1.025
Styxosaurus 'A'	SDSM 451	45	119	85	92	97.18	134.5	-0.872	1.033
Styxosaurus 'A'	SDSM 451	46	117	85	92	96.64	132.2	-0.86	0.954
Styxosaurus 'A'	SDSM 451	47	118	82	95	96.79	133.3	-0.865	0.939
Styxosaurus 'A'	SDSM 451	48	120	86	91	97.48	135.6	-0.878	1.091
Styxosaurus 'A'	SDSM 451	49	115	92	110	104.70	113.9	-1.042	0.156
Styxosaurus 'A'	SDSM 451	52	114	81	123	103.85	111.8	-1.031	-0.07
Styxosaurus 'A'	SDSM 451	53	110	93	110	103.53	108.4	-1.019	-0.068
Styxosaurus 'A'	SDSM 451	54	115	93	117	107.26	109.5	-1.097	-0.067
Styxosaurus 'A'	SDSM 451	55	112	87	123	105.73	106.7	-1.07	-0.259
Styxosaurus 'A'	SDSM 451	56	111	94	131	110.46	98.7	-1.167	-0.627
Styxosaurus 'A'	SDSM 451	57	106	91	137	109.22	93.0	-1.146	-0.944
Styxosaurus 'A'	SDSM 451	58	102	90	144	109.23	87.2	-1.15	-1.275
Styxosaurus 'A'	SDSM 451	59	104	85	135	105.58	94.5	-1.073	-0.883
Styxosaurus 'A'	SDSM 451	60	98	94	140	108.34	83.8	-1.131	-1.432
Styxosaurus 'A'	SDSM 451	61	97	86	144	105.81	84.3	-1.082	-1.442
Brancasaurus	unknown	3	16	18	22	18.50	80.0	2.737	-1.243
Brancasaurus	unknown	4	17	18	23	19.16	82.9	2.66	-1.108
Brancasaurus	unknown	5	20	20	25	21.54	88.9	2.407	-0.785
Brancasaurus	unknown	6	20	22	26	22.53	83.3	2.309	-1.058
Brancasaurus	unknown	7	20	21	26	22.18	85.1	2.342	-0.989
Brancasaurus	unknown	8	22	24	26	23.94	88.0	2.181	-0.742
Brancasaurus	unknown	9	25	25	27	25.64	96.2	2.033	-0.331
Brancasaurus	unknown	10	24	25	28	25.60	90.6	2.034	-0.644
Brancasaurus	unknown	11	25	26	29	26.60	90.9	1.95	-0.629
Brancasaurus	unknown	12	26	27	30	27.61	91.2	1.87	-0.616
Brancasaurus	unknown	13	28	31	31	29.96	90.3	1.695	-0.584
Brancasaurus	unknown	14	30	30	32	30.64	96.8	1.645	-0.32
Brancasaurus	unknown	15	30	30	33	30.96	95.2	1.622	-0.423
Brancasaurus	unknown	16	32	31	34	32.30	98.5	1.53	-0.27
Brancasaurus	unknown	17	33	33	35	33.64	97.1	1.442	-0.316
Brancasaurus	unknown	18	35	33	38	35.26	98.6	1.337	-0.317
Brancasaurus	unknown	19	35	33	38	35.26	98.6	1.337	-0.317
Brancasaurus	unknown	20	36	34	39	36.26	98.6	1.276	-0.317
Brancasaurus	unknown	21	37	35	38	36.63	101.4	1.257	-0.144
Brancasaurus	unknown	22	40	36	38	37.95	108.1	1.182	0.178
Brancasaurus	unknown	23	39	36	41	38.60	101.3	1.141	-0.195
Brancasaurus	unknown	24	41	37	42	39.93	103.8	1.068	-0.083
Brancasaurus	unknown	25	41	38	42	40.28	102.5	1.049	-0.122
Brancasaurus	unknown	26	41	40	43	41.30	98.8	0.995	-0.278
Brancasaurus	unknown	27	45	40	42	42.27	109.8	0.948	0.237
Brancasaurus	unknown	28	43	41	45	42.95	100.0	0.909	-0.244
Brancasaurus	unknown	29	42	43	44	42.98	96.6	0.909	-0.349
Brancasaurus	unknown	30	44	44	44	43.98	100.0	0.86	-0.166

Taxon	**Spec. #**	**Position**	**L**	**H**	**B**	**GM**	**VLI**	**lnPC1**	**lnPC2**
Brancasaurus	unknown	31	45	43	49	45.58	97.8	0.778	-0.388
Brancasaurus	unknown	33	45	44	50	46.24	95.7	0.746	-0.49
Brancasaurus	unknown	34	44	46	50	46.58	91.7	0.73	-0.661
Brancasaurus	unknown	35	40	46	52	45.72	81.6	0.766	-1.238
Brancasaurus	unknown	36	42	46	53	46.77	84.8	0.717	-1.074
Brancasaurus	unknown	37	40	45	56	46.52	79.2	0.725	-1.454
Mauisaurus	ZFR 115	3	32	25	36	30.64	104.9	1.639	-0.142
Mauisaurus	ZFR 115	4	33	26	39	32.21	101.5	1.528	-0.325
Mauisaurus	ZFR 115	5	34	26	40	32.81	103.0	1.488	-0.27
Mauisaurus	ZFR 115	6	35	28	43	34.79	98.6	1.359	-0.487
Mauisaurus	ZFR 115	7	35	27	42	34.10	101.4	1.403	-0.354
Mauisaurus	ZFR 115	8	35	28	44	35.05	97.2	1.342	-0.564
Mauisaurus	ZFR 115	9	36	29	45	36.07	97.3	1.28	-0.56
Mauisaurus	ZFR 115	10	39	30	48	38.28	100.0	1.15	-0.453
Mauisaurus	ZFR 115	11	40	30	48	38.61	102.6	1.132	-0.334
Mauisaurus	ZFR 115	12	42	31	49	39.94	105.0	1.059	-0.224
Mauisaurus	ZFR 115	13	43	33	52	41.93	101.2	0.952	-0.406
Mauisaurus	ZFR 115	14	42	32	51	40.91	101.2	1.005	-0.406
Mauisaurus	ZFR 115	15	43	34	53	42.62	98.9	0.916	-0.515
Mauisaurus	ZFR 115	16	46	36	53	44.42	103.4	0.828	-0.284
Mauisaurus	ZFR 115	17	44	37	53	44.17	97.8	0.84	-0.533
Mauisaurus	ZFR 115	18	52	37	57	47.85	110.6	0.667	0.004
Mauisaurus	ZFR 115	19	51	36	57	47.11	109.7	0.7	-0.046
Mauisaurus	ZFR 115	20	54	39	59	49.88	110.2	0.577	-0.013
Mauisaurus	ZFR 115	21	56	40	60	51.20	112.0	0.52	0.063
Mauisaurus	ZFR 115	22	56	41	60	51.63	110.9	0.503	0.026
Mauisaurus	ZFR 115	23	58	42	63	53.52	110.5	0.424	-0.009
Mauisaurus	ZFR 115	24	58	44	63	54.35	108.4	0.39	-0.078
Mauisaurus	ZFR 115	25	60	44	64	55.26	111.1	0.355	0.027
Mauisaurus	ZFR 115	26	62	47	68	58.28	107.8	0.238	-0.121
Mauisaurus	ZFR 115	27	61	45	66	56.56	109.9	0.303	-0.032
Mauisaurus	ZFR 115	28	65	48	69	59.91	111.1	0.179	0.02
Mauisaurus	ZFR 115	29	68	51	70	62.36	112.4	0.093	0.092
Mauisaurus	ZFR 115	30	66	49	70	60.92	110.9	0.142	0.012
Mauisaurus	ZFR 115	31	65	42	68	57.02	118.2	0.285	0.267
Mauisaurus	ZFR 115	32	70	53	72	64.38	112.0	0.024	0.076
Mauisaurus	ZFR 115	33	71	54	75	65.98	110.1	-0.031	-0.022
Mauisaurus	ZFR 115	34	73	55	74	66.70	113.2	-0.053	0.126
Mauisaurus	ZFR 115	35	72	57	77	68.08	107.5	-0.099	-0.125
Mauisaurus	ZFR 115	36	73	58	79	69.39	106.6	-0.141	-0.173
Mauisaurus	ZFR 115	37	74	61	77	70.28	107.2	-0.167	-0.098
Mauisaurus	ZFR 115	38	74	57	76	68.41	111.3	-0.108	0.047
Mauisaurus	ZFR 115	39	75	58	81	70.60	107.9	-0.179	-0.13
Mauisaurus	ZFR 115	40	76	62	82	72.80	105.6	-0.245	-0.208
Mauisaurus	ZFR 115	41	76	64	84	74.17	102.7	-0.287	-0.336
Mauisaurus	ZFR 115	42	77	63	85	74.40	104.1	-0.294	-0.292

Taxon	**Spec. #**	**Position**	**L**	**H**	**B**	**GM**	**VLI**	**lnPC1**	**lnPC2**
Mauisaurus	ZFR 115	43	78	63	85	74.72	105.4	-0.303	-0.231
Mauisaurus	ZFR 115	44	83	73	80	78.52	108.5	-0.404	0.044
Mauisaurus	ZFR 115	45	80	66	88	77.42	103.9	-0.38	-0.298
Mauisaurus	ZFR 115	46	80	68	89	78.49	101.9	-0.41	-0.381
Mauisaurus	ZFR 115	47	80	68	90	78.78	101.3	-0.419	-0.418
Mauisaurus	ZFR 115	48	80	69	90	79.17	100.6	-0.429	-0.44
Mauisaurus	ZFR 115	50	78	72	97	81.63	92.3	-0.499	-0.873
Mauisaurus	ZFR 115	51	77	71	95	80.35	92.8	-0.464	-0.842
Mauisaurus	ZFR 115	52	80	74	94	82.22	95.2	-0.512	-0.69
Mauisaurus	ZFR 115	53	83	74	95	83.53	98.2	-0.546	-0.553
Mauisaurus	ZFR 115	54	81	75	96	83.51	94.7	-0.547	-0.722
Mauisaurus	ZFR 115	55	81	74	94	82.56	96.4	-0.521	-0.631
Mauisaurus	ZFR 115	56	81	76	93	83.00	95.9	-0.532	-0.635
Mauisaurus	ZFR 115	57	79	76	100	84.32	89.8	-0.57	-0.995
Mauisaurus	ZFR 115	58	80	75	101	84.59	90.9	-0.577	-0.95
Mauisaurus	ZFR 115	59	78	76	100	83.97	88.6	-0.561	-1.055
Mauisaurus	ZFR 115	60	77	75	100	83.24	88.0	-0.543	-1.096
Mauisaurus	ZFR 115	61	77	80	101	85.33	85.1	-0.596	-1.225
Mauisaurus	ZFR 115	62	74	80	101	84.21	81.8	-0.569	-1.411
Mauisaurus	ZFR 115	63	76	84	101	86.35	82.2	-0.622	-1.358
Mauisaurus	ZFR 115	64	75	80	102	84.86	82.4	-0.586	-1.381
Mauisaurus	ZFR 115	65	75	80	98	83.74	84.3	-0.555	-1.247