

## CRANIAL ALLOMETRY IN *COELOPHYSIS*: PRELIMINARY RESULTS

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### ABSTRACT

A statistical analysis of twelve *Coelophysis bauri* skulls from Ghost Ranch has been attempted incorporating bivariate and principal components techniques to search for allometric characteristics and consistent variation that might be attributable to systematic differences in the sample. The expected allometric patterns were observed in the eigenvectors of the first three principal components. The sample size is too small for well-defined clusters in the principal component plots, but as it increases, the allometric equations are not expected to change significantly.

### INTRODUCTION

The famous sample of small theropods, referred to *Coelophysis bauri*, from the upper Triassic Ghost Ranch Quarry of New Mexico was described by Colbert (1989). In his monograph, he focused on two specimens, AMNH 7223 and 7224, although photographs were included of other skulls. In this paper, and his later book (Colbert, 1995), Colbert discussed the geology and taphonomy of the site as interpreted by Schwartz and Gillette (1995), the history of collections there, and the eventual disposition of the blocks, as well as the anatomy and paleobiology of *Coelophysis*. Schwartz and Gillette interpret the deposit as resulting from the catastrophic death of a theropod population and subsequent fluvial concentration and burial a short time later.

*Coelophysis* and closely related theropods have also been recovered from other sites. A partial specimen has been recovered from the Petrified Forest of northern Arizona (Padian, 1986). Another small theropod, *Podokesaurus holyokensis*, was found in a boulder in Massa-

chusetts (Talbot, 1911). The original material was destroyed, but casts are available at the American Museum of Natural History and the Yale-Peabody Museum. Colbert (1964) synonymized *Podokesaurus* and *Coelophysis*, but Olsen noted the characters that he used were primitive (in Weishampel and Young, 1996), so *Podokesaurus* has been retained, since it does have some unique characters. A very similar theropod *Syntarsus rhodesiensis*, from the lower Jurassic Forest Sandstone of Zimbabwe is represented by a considerable sample of reasonably complete skeletons that exhibit some degree of variability (Raath, 1969, 1990). A theropod skull from the lower Jurassic Kayenta Formation of Arizona has been referred to as *Syntarsus kayentakatae* (Rowe, 1989). If *Syntarsus* was present at Ghost Ranch, it would mean that this genus survived the Triassic-Jurassic extinction event.

Historically, Colbert has recognized the presence of only one species at Ghost Ranch, *Coelophysis bauri*, that exhibits some degree of variation (Colbert, 1989). There has been some concern and later contention regarding the practice of erecting a new taxon on the basis of

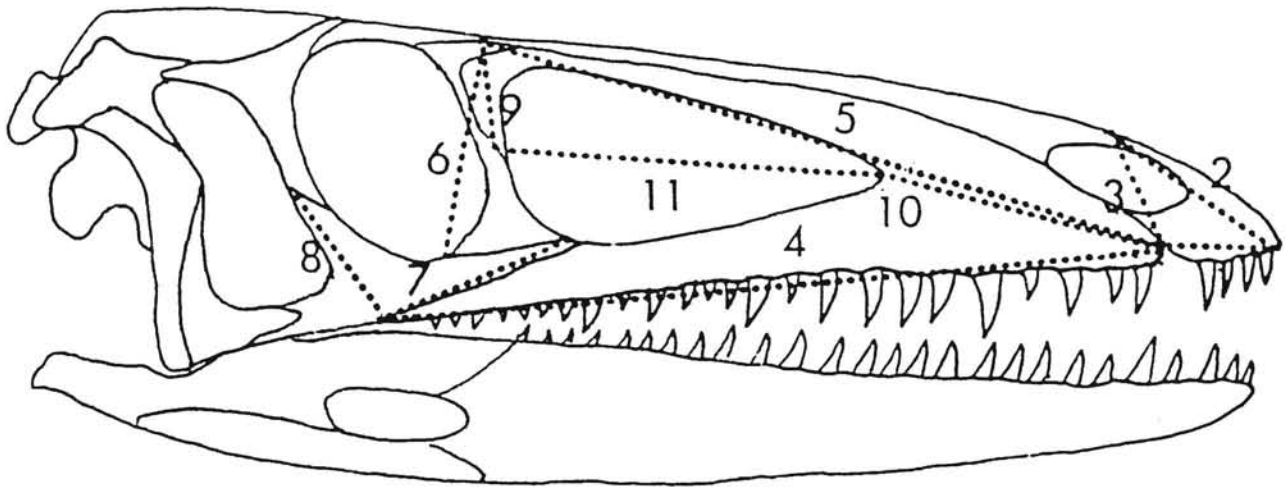


Figure 1. Landmarks for *Coelophysis bauri* cranial data (after Colbert, 1989).

inadequate type material (AMNH 2722) (Padian, 1986). Given the perceived inadequacy of the type material and the question of its actually having been derived from the Ghost Ranch Quarry, Hunt and Lucas (1991) erected a new species, *Rioarribasaurus colberti*, with AMNH 7224 designated the holotype. However, the International Commission on Zoological Nomenclature has ruled that this term is invalid. Colbert, (1990) follows Simpson (1945) in that the original material serves only as a name holder. Simpson (1945) indicated that the type may not be a representative specimen of the species and may not even be diagnostic. Paul (1993) synonymized the Ghost Ranch theropod with *Syntarsus*. Sullivan (pers. com., 1996) argues that there are at least three distinct theropods within the Ghost Ranch sample that he tentatively refers to as *Coelophysis*, *Rioarribasaurus*, and *Syntarsus*. He is currently working on an extended description of the skull morphology of the Ghost Ranch material.

Within the Ghost Ranch *Coelophysis* sample, there are at least two skull morphologies present that can be most readily distinguished by the development of vertical crests above the orbit

and running anteriorly (Currie, pers. com., 1996 and later verified). Colbert (1990) noted differing limb and neck proportions in different individuals and variable degrees of tarsal fusion that were apparently not related to age. Whether the postcranial variation is consistent with the development of supraorbital crests is unclear.

Preliminary results of a statistical analysis searching for patterns of variation and describing allometric changes within a sample of Ghost Ranch skulls are presented. For this discussion, all of the Ghost Ranch material will be referred to as *Coelophysis bauri*, following Colbert.

## MATERIALS AND METHODS

Preliminary bivariate and multivariate statistical analyses have been performed using morphometric data taken from a sample of twelve *Coelophysis* skulls housed at the Museum of Northern Arizona, the American Museum of Natural History, Ghost Ranch, the Harvard Museum of Comparative Zoology, and the Royal Tyrell Museum of Paleontology. The landmarks were defined (Figure 1) using a skull housed at the Museum of Northern Arizona (MNA

| Variable | (ln) mean | (ln) range  | (ln) St. Dev. | W     | (ln) CV | $\hat{\alpha}$ | $\hat{\beta}$ |
|----------|-----------|-------------|---------------|-------|---------|----------------|---------------|
| M1       | 2.594     | 2.197-3.020 | 0.292         | 0.915 | 11.272  | 0.363          | 1.226         |
| M2       | 3.052     | 2.251-3.277 | 0.368         | 0.922 | 12.053  | 0.571          | 0.092         |
| M3       | 2.639     | 2.116-3.714 | 0.485         | 0.887 | 18.360  | 0.610          | 0.342         |
| M4       | 4.322     | 3.611-4.998 | 0.513         | 0.912 | 11.870  | 0.791          | 1.342         |
| M5       | 4.181     | 3.535-4.822 | 0.508         | 0.872 | 12.162  | 0.791          | 1.201         |
| M6       | 3.199     | 2.565-3.714 | 0.346         | 0.952 | 10.828  | 0.461          | 1.462         |
| M9       | 2.594     | 1.808-3.273 | 0.489         | 0.955 | 18.871  | 0.350          | 1.276         |
| M10      | 3.064     | 2.186-3.963 | 0.520         | 0.986 | 16.957  | 0.657          | 0.588         |
| M11      | 3.765     | 2.766-4.407 | 0.574         | 0.907 | 15.247  | -              | -             |

**Table 1.** Univariate and bivariate statistics for *Coelophysis* crania. Reconstructed sample size is 12. All statistics are calculated from natural log-transformed variables. M1-M11 measurements correspond to Figure 1. Variables M7 and M8 have been deleted. W: Wilke-Shapiro normality test. CV: Coefficient of Variation.  $\alpha$ : estimated slope.  $\beta$ : intercept. The variable lacking values represents the x-axis for the regressions.

V3315). All analyses were performed with SAS on the University of Arizona VMS system. A total of eleven measurements were taken from each specimen, when possible, but only nine are retained for the analysis, as #7 and #8 were rarely preserved. Otherwise, missing data are estimated following previous bivariate regression methods (Smith, in press). This procedure has the unfortunate property of decreasing the apparent variability (Dodson, 1975) that is being searched for, but permits, in this case, data from a representative number of specimens. The data were then converted to natural logs to more closely follow ontogeny (Bookstein, et al. 1985).

The program that was used to analyze variation in *Allosaurus* (Smith, in press) was revised to describe univariate, bivariate, and multivariate characteristics of the *Coelophysis* data. Frequencies, univariate descriptive statistics, and Wilke-Shapiro normality tests were computed for each log-transformed variable (Table 1). A Principal Components Analysis extracted from a covariance matrix is used to maximize within group variation. This method

requires that the data be entered as a single group, but is not sensitive to multivariate normality (Rencher, 1995). Because the covariance matrix is not inverted in this process, the number of variables can exceed the number of observations without the matrix becoming singular.

The loadings within the individual eigenvectors for each principal component are used to form contrasts to describe allometry within the skulls (Table 2). Only those with relatively absolute high values are retained for this process, while those close to '0' were dropped. As will be noted later, the first principal component is interpreted as a size vector. The number of significant components is interpreted as those with identifiable loading patterns. The two variables that had the lowest loading values on the first principal component were used to compute bivariate regressions. Plots of principal component II versus I (Figure 2), principal component II versus III (Figure 3), and the bivariate regression (Figure 4) were used to search for significant ontogenetic trends or clustering.

| Variable | PC I  | PC II  | PC III |
|----------|-------|--------|--------|
| M1       | 0.209 | 0.168  | -0.399 |
| M2       | 0.266 | 0.066  | -0.081 |
| M3       | 0.323 | 0.371  | -0.503 |
| M4       | 0.413 | -0.115 | 0.040  |
| M5       | 0.416 | -0.028 | 0.078  |
| M6       | 0.246 | 0.102  | 0.200  |
| M9       | 0.260 | 0.651  | 0.624  |
| M10      | 0.343 | -0.559 | 0.463  |
| M11      | 0.438 | -0.264 | -0.295 |
| Eigenval | 1.468 | 0.181  | 0.155  |
| Prop.    | 0.758 | 0.094  | 0.080  |

**Table 2.** Multivariate statistics for *Coelophysis* crania. Reconstructed sample size is 12. The Principal Components Analysis is extracted from a covariance matrix. Variables M7 and M8 have been deleted. Total variability explained is 93%.

## RESULTS

Although a reasonable allometric range of individuals has been obtained, the size distribution is non-normal (Table 1). Distinct patterns are observed in the loadings of the first three principal components (Table 2). Principal component I explains 76% of the observed variation. All of the loadings are significant and positive, indicating that it can be regarded as a size component. The second describes the inverse relationship between the length of the snout and the height of the skull. This result means that, as the length of the toothrow increases, the relative height of the postorbital region decreases. Another 9% of the observed variation can be attributed to this component. The third principal component describes variation in the antorbital fenestra and external nares. It explains a further 8% of the observed variation. These three components account for 93% of the observed variation.

The variables selected for the bivariate regression are the distance from the anterior end of the premaxilla to the contact with the nasal (#2) and the height of the postorbital (#6) (Figure 1). A single allometric trend is apparent (Figure 4). The slope ( $\alpha$ ) and intercept ( $\beta$ ) were estimated to be 0.241 and 0.736, respectively. This regression has an  $R^2$  value of 0.760. The correlations among the other variables are very high, permitting least squares estimates of the slopes ( $\alpha$ ) and intercepts ( $\beta$ ) (Table 1). This regression method makes the unlikely assumption that there is no measurement error in the x-axis, but corresponds fairly well with method II techniques such as Reduced Major Axis (Sokal and Rohlf, 1995).

Multivariate (Figures 2 and 3) and bivariate (Figure 4) plots failed to reveal any significant clustering, but the sample size is too low to reveal any pronounced variation that can be attributed to systematic differences. However, the two outliers in the bivariate plot are tantalizing. As more observations are added to the data matrix, they may indicate a systematic difference following a distinct allometric trajectory.

## DISCUSSION

The statistical analysis for *Coelophysis bauri* skulls has revealed the expected allometric results. They exhibit a fairly high degree of individual variation, but no significant clustering is observed in any of the plots. As the sample size increases, the allometric relations are not expected to change significantly, but it is probably too low to use these results to support the presence of multiple taxa at Ghost Ranch. This conclusion may be altered as the *Coelophysis* data set is increased and *Syntarsus* data is added. Once these data are obtained, they will be incorporated into a larger principal

# Coelophysis Crania

## PCA Plot

Natural Log Transformed Data

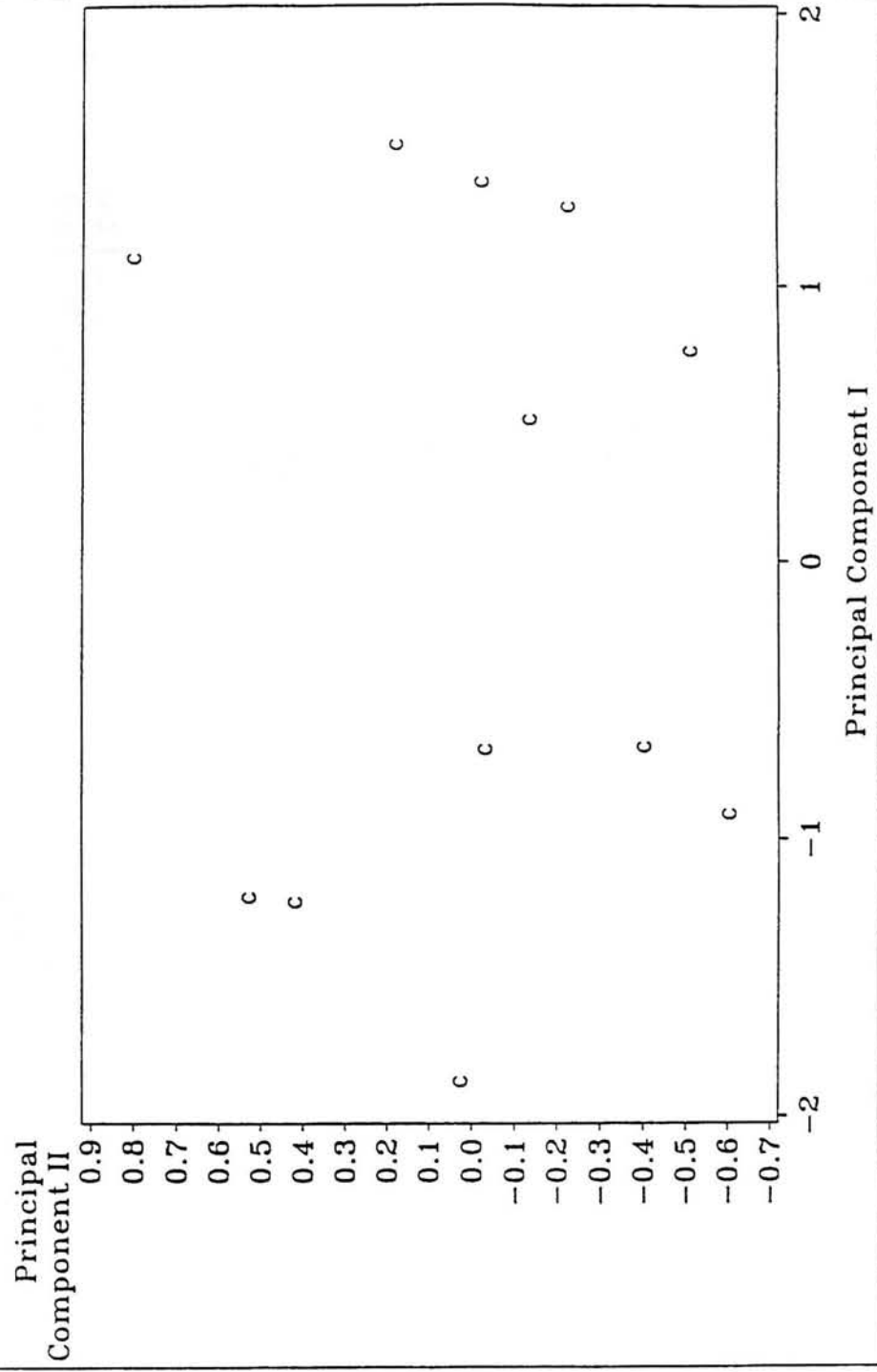


Figure 2. Plot of Principal Component II versus Principal Component I.

# Coelophysis Crania

## PCA Plot

Natural Log Transformed Data

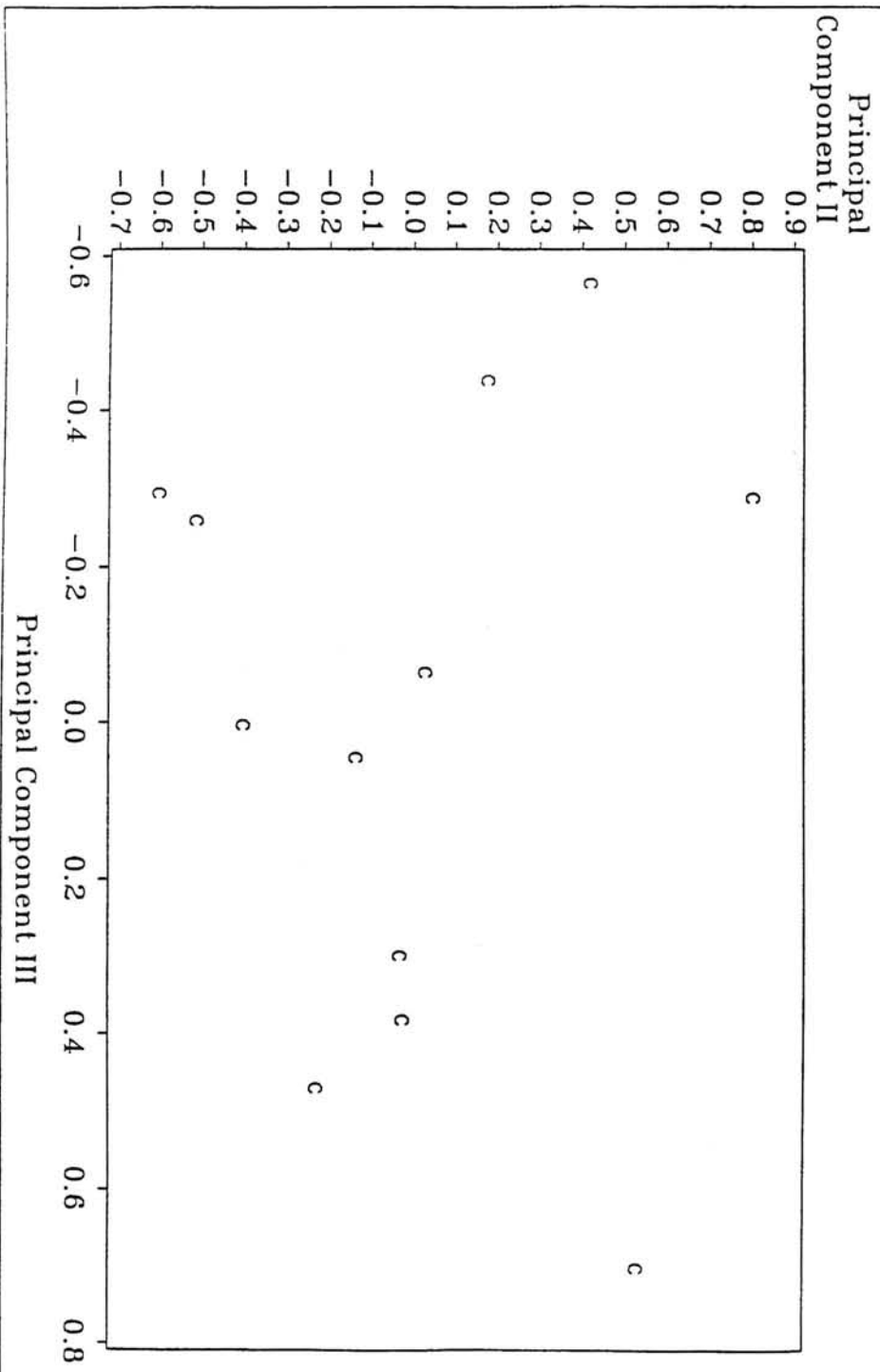


Figure 3. Plot of Principal Component II versus Principal Component III.

components Analysis. A discriminant Analysis will then be attempted using the recognized taxa as the functional units. If *Syntarsus* is shown to be present at Ghost Ranch, it would indicate that this theropod was one of the few dinosaurs that crossed the Triassic-Jurassic boundary.

## ACKNOWLEDGMENTS

Ralph Chapman and Peter Dodson provided much encouragement and their comments have been invaluable. I also thank all those people who provided access and, in some cases, accommodations while I was collecting the morphometric data. They include Ned Colbert and Mike Morales (Museum of Northern Arizona), Don Brinkman and Phil Currie (Royal Tyrell Museum of Paleontology), Alex Downs and Lynette Gillette (Ghost Ranch), and Charlotte Holton (American Museum of Natural History). Financial support for this project while in New York was provided by an AMNH collections studies grant. Ned Colbert and Spencer Lucas (New Mexico Museum of Natural History and Science) reviewed the manuscript.

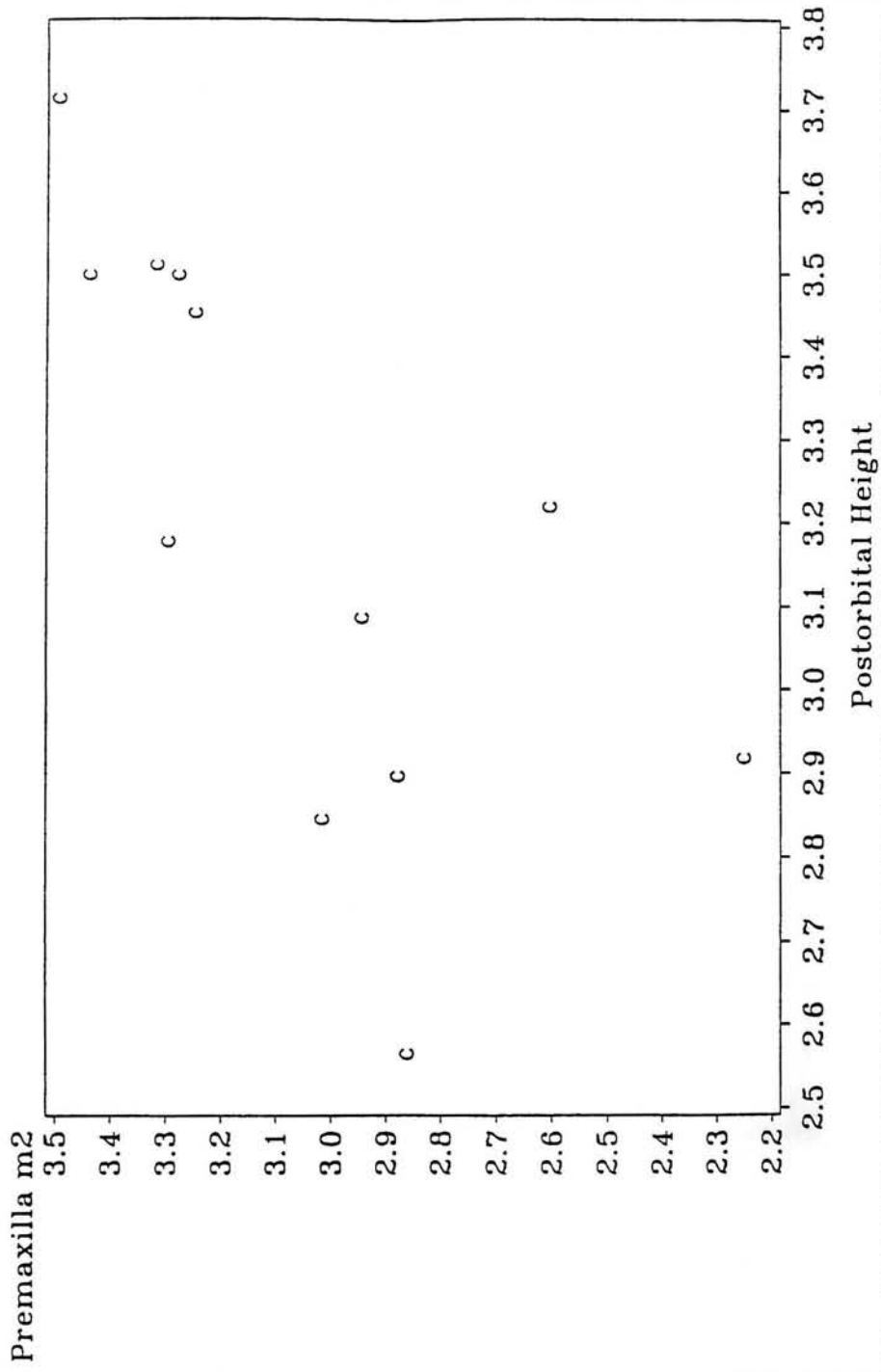
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# Coelophysis Crania

## Bivariate Plot

Natural Log Transformed Data



**Figure 4.** Bivariate plot of postorbital height versus premaxilla measurement 2. Parameter estimates are  $\alpha$  (slope) = 0.736,  $\beta$  (intercept) = 0.241, and  $R^2 = 0.760$ .