

FACIAL VARIATION IN *COELOPHYSIS BAURI* AND THE STATUS OF *MEGAPNOSAURUS (SYNTARSUS)*

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Abstract—A considerable amount of variation is observed within the theropod sample from the Ghost Ranch Quarry within the Upper Triassic upper Petrified Forest Member of the Chinle Formation in north-central New Mexico. The meaning of this variation was unclear, but has been generally considered a result of ontogenetic, sexual, or systematic differences. Historically, these specimens have been referred to a single species, *Coelophysis bauri*. Twenty-three *Coelophysis bauri* skulls from Ghost Ranch and one of *Megapnosaurus (Syntarsus) kayentakatae*, from the Lower Jurassic Kayenta Formation of northern Arizona, were measured to create a morphometric database in order to conduct statistical analyses. *Megapnosaurus (Syntarsus) kayentakatae* data were included in the *C. bauri* matrix for comparative purposes. The systematic position of the Kayenta material is in flux and may change in the future (R. Tykoski, personal commun., 2005). Despite the considerable taphonomic distortion, a meaningful biological signal is present in the multivariate data. PC I is interpreted as a size vector. PC II is a contrast between the height and length of the skull. PC III is a contrast between the maxilla and premaxilla. The results indicate that a single variable species is present at Ghost Ranch that is distinct at the generic level from *Megapnosaurus (Syntarsus) kayentakatae*. Two morphs were identified within the Ghost Ranch sample. They might be regarded as male and female, but a specific designation is not warranted.

INTRODUCTION

A large theropod sample is available from the well known Upper Triassic Ghost Ranch Quarry of New Mexico. Historically, all of the theropods in this sample have been assigned to *Coelophysis bauri* (Colbert, 1989). The collection consists of hundreds of disarticulated bones, skulls, and partial to nearly complete small to large theropod skeletons. Early juveniles have not been reported, although some very small bones are present that have not been recognized as theropod (J. Harris, personal commun., 2006). Many of the postcranial bones are undistorted, although most of the skulls have been laterally flattened along sutures. Therefore, the individual skull bones are often reasonably undistorted. Other vertebrate taxa represented at the quarry include fish and a number of primitive archosaurs, including *Hesperosuchus*, *Redondasaurus*, and *Vancleaveia*, among others (Lucas et al., 2005).

TAPHONOMIC SETTING

The Ghost Ranch Quarry is in a fluvial siltstone deposit in the Norian upper Petrified Forest Member of the Chinle Formation (Colbert, 1989). The accumulation of theropods at Ghost Ranch is generally considered a catastrophic deposit (Schwartz and Gillette, 1994). They find no evidence for either volcanism, as had been previously proposed (Colbert, 1947), or predator entrapment (Bakker, 1986) as at the Cleveland-Lloyd Dinosaur Quarry, Utah (Richmond and Morris, 1996). Schwartz and Gillette (1994) cite the lack of bentonitic layers as evidence that a volcanic eruption did not cause the burial. They note a specimen age range approximating a normal distribution in the Ghost Ranch Quarry that is not indicative of a predator trap. An almost complete ontogenetic range, traditionally regarded as being derived from a single theropod taxon, is present in Ghost Ranch, whereas, like more recent traps (Richmond and Morris, 1997, 1998), Cleveland-Lloyd is dominated by juvenile to sub-adult allosaurs (Smith, 1998). The catastrophic model that Schwartz and Gillette (1994) propose is a drought-induced mass-death assemblage more similar to what has been proposed for the Dry Mesa Dinosaur Quarry (Richmond and Morris, 1998), although the faunal diversity of Dry Mesa (Smith, 1997a) might be considered anomalously high for such an assemblage (Schwartz and Gillette, 1994).

TAXONOMY OF THE GHOST RANCH THEROPOD

The Ghost Ranch theropod accumulation has usually been considered monotypic, consisting of only one, morphologically variable, species: *Coelophysis bauri* (Colbert, 1989). Cope (1889) erected two other species of *Coelophysis*, *C. longicollis* and *C. willistoni*, in addition to a series of other genera, based upon material from the region close to Ghost Ranch, but these are currently recognized as synonyms for *C. bauri* (Colbert, 1989). However, there is concern that the type (AMNH 2722), consisting of four sacral vertebrae and a partial ilium, as originally described (Cope, 1889), lacks preserved synapomorphies that would permit the specimen to represent a diagnosable taxon (Padian, 1986). Postcranial theropod material from the Chinle Formation in Petrified Forest of Arizona was described by Padian (1986) and referred to *Coelophysis bauri*, despite his misgivings about validity of the name, given that it is based on non-diagnosable material. Colbert (1989, 1990, 1995), however, followed Simpson (1945) in arguing that the original material only serves to hold the name even if it may not be representative or even diagnostic. Noting the fragmentary nature of the of the holotype of *Coelophysis bauri*, a new species, *Rioarribasaurus colberti* was erected for the Ghost Ranch theropod sample, based on the well-preserved skeleton, AMNH 7224 (Hunt and Lucas, 1991). Subsequently, Colbert et al. (1992) had the name and type specimen of *Coelophysis bauri* reassigned to AMNH 7224, rendering the name *Rioarribasaurus colberti* unnecessary.

Syntarsus rhodesiensis, a small theropod very similar to *Coelophysis bauri*, was described from a collection of specimens from the Lower Jurassic Forrest Sandstone of Zimbabwe (Raath, 1969). As the genus name *Syntarsus* was preoccupied by a beetle, the African theropod was renamed *Megapnosaurus*, but this term has only been used sporadically (Ivie et al., 2001). Characters that ostensibly separate *Megapnosaurus (Syntarsus) rhodesiensis* from *Coelophysis bauri* included an accessory nasal foramen, the lacrimal/jugal contact, the dimensions of the antorbital fenestra, and a differing amount of tarsal fusion, among others (Raath, 1969, 1990; Tykoski, 1998; Bristowe and Raath, 2004). Using a recently described skull from Zimbabwe, Bristowe and Raath regard all of these characters as incorrect or inadequate for a generic distinction. They also subsumed the New England form *Podokesaurus*

holyokensis within *Coelophysis*. There are, however, no derived characters to support this synonymy, so *Podokesaurus* should be retained as generically distinct.

Many workers regard the Ghost Ranch theropod as sufficiently similar to *Megapnosaurus* (*Syntarsus*) *rhodesiensis* for the two to be synonymized: Paul (1993) referring to the Ghost Ranch theropod as *Syntarsus colberti* and Downs (2000) referred to the African material as *Coelophysis rhodesiensis*. Most recently, Bristowe and Raath (2004) referred *Megapnosaurus* (*Syntarsus*) *rhodesiensis* and *M. (S.) kayentakatae* to *Coelophysis*. Conversely, Sullivan et al. (1996) contended that the original material collected by Baldwin near Orphan Mesa, a site stratigraphically lower than the Ghost Ranch Quarry, plus other bones collected in the Arroyo del Yeso south of the quarry by the State Museum of Pennsylvania and the New Mexico Museum of Natural History and Science, should be the only specimens that can be referred to *Coelophysis*. They further argue that the Ghost Ranch Quarry dinosaurs are *Rioarribasaurus colberti* and *Coelophysis* sp., with a third, morphologically distinct, theropod possibly present and that these are distinct from *Coelophysis bauri*.

Coelophysid material from Orphan Mesa, close to Ghost Ranch, along with the pubis (AMNH 2706) originally placed in *Coelophysis longicollis*, was recently referred to the new species *Eucoelophysis baldwini* (Sullivan and Lucas, 1999). Fragmentary coelophysid material also referred to *Eucoelophysis* was found at the Snyder Quarry (Heckert et al., 2003), which is stratigraphically lower than Ghost Ranch. Additionally, a large coelophysid theropod from eastern New Mexico in exposures of the Upper Triassic Dockum Group was called *Gojirasaurus* (Carpenter, 1997). An additional specimen of *Coelophysis* sp. (?) consisting of the sacrum, pelvis, and some dorsal vertebrae was recently noted from a Triassic (?) fissure fill in Great Britain (Rauhut and Hungerbühler, 2000). It was found close to the material from *Thecodontosaurus*. None of this material was included in this analysis, because there was no skull material preserved.

Colbert (1989) placed *Coelophysis* within the family Podokesauridae, but the characters used to unite this group are primitive, as also noted by Olsen (in Weishampel and Young, 1996). A better term, with a revised diagnosis, would probably be Coelophysidae (Holtz, 2000), presumably a holophyletic clade, if limited to *Coelophysis*, *Megapnosaurus* (*Syntarsus*), and the fragmentary taxa.

MORPHOMETRICS AND VARIATION

Gracile and robust individuals within the *Megapnosaurus* (*Syntarsus*) *rhodesiensis* sample were identified based primarily on limb proportions and variation, with this variation considered a result of possible sexual dimorphism. Raath (1990) regarded the robust form as the female from comparison with modern raptorial birds, although this allocation is arbitrary. The Jurassic form *Megapnosaurus* (*Syntarsus*) *kayentakatae* consists, in part, of a skull from the Kayenta Formation of Arizona (Rowe, 1989; Tykoski, 1998). Morphometric data were collected from the postcranial material of *Coelophysis bauri*, *Megapnosaurus* (*Syntarsus*) *rhodesiensis*, and *Podokesaurus holyokensis*, and these results will be presented in a forthcoming paper.

The presence of morphometric and morphological variation within the theropod sample from Ghost Ranch has long been noted (Colbert, 1990), although the meaning of this variation was not clear. Possible biological sources include ontogenetic, systematic, sexually dimorphic, and/or individual variation. There are differences in limb and neck proportions and variation in the degree of tarsal fusion that is unrelated to age (Colbert, 1990, 1995). Additionally, the presence of a lacrimal crest from the orbit to the nares has been suggested (P. Currie, personal commun., 1996). However, if this crest exists, and if there is variation in this character, it is subtle and hard to distinguish from the distortion that is frequently present in the skulls (following A. Downs, personal commun., 1996). The updated skull morphology, presumably including a discus-

sion of this crest is expected in a forthcoming study (R. Sullivan, personal commun., 1997).

This paper adds to the previous results of a morphometric analysis of Ghost Ranch theropod skulls (Smith, 1997b) that was undertaken to detect shape differences within the sample. The sample size has been increased from twelve to twenty-four skulls of various sizes from juvenile to adult. Data from a cast of theropod skull from the Lower Jurassic Kayenta Formation of Arizona, *Megapnosaurus* (*Syntarsus*) *kayentakatae* (Rowe, 1989) were included to attempt to morphometrically distinguish the two genera. As in a statistical analysis of *Allosaurus* (Smith, 1998, 1999), univariate, bivariate, and multivariate techniques were combined to describe and determine the amount of variation. Sources of that variation and its meaning are proposed. Additionally, if *Coelophysis* is regarded as present in the Jurassic of Arizona and Africa, it would also indicate that this consequently widespread genus crossed the Triassic-Jurassic boundary with minimal change.

Abbreviations: AMNH, American Museum of Natural History, New York, New York; BYU, Brigham Young University, Provo, Utah; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CIMNH, Cleveland Museum of Natural History, Cleveland, Ohio; DNM, Dinosaur National Monument, Utah; DSC, Dixie State College, St. George, Utah; ISU, Idaho State University, Pocatello, Idaho; MCZ, Harvard Museum of Comparative Zoology, Boston, Massachusetts; MNA, Museum of Northern Arizona, Flagstaff, Arizona; NMNH, National Museum of Natural History, Washington, DC; RHMP, Ghost Ranch Museum of Paleontology, Abiquiu, New Mexico; RTMP, Royal Tyrell Museum of Paleontology, Drumheller, Alberta; SMP, State Museum of Pennsylvania, Harrisburg, Pennsylvania; UB, University of Bridgeport, Bridgeport, Connecticut; UP, University of Pennsylvania, Philadelphia, Pennsylvania; YPM, Yale-Peabody Museum, New Haven, Connecticut; WC, Westminster College, Salt Lake City, Utah.

MATERIALS AND METHODS

Landmarks that would be readily located in other skulls while also suitably describing the skull were selected based upon a specimen at the Museum of Northern Arizona (MNA V3315) (Fig. 1). Based on previous theropod results, the facial region of the skull was expected to show the most variation (Smith, 1998, 1999), so landmarks were concentrated in that region. The data were collected with calipers and a tape measure on a sample of twenty original skulls of *Coelophysis bauri*. Measurements from three casts were included in the data matrix: two from *Coelophysis*, AMNH 7224 and CMNH 1374, and one of *Megapnosaurus* (*Syntarsus*) *kayentakatae*, NMNH 44240. All measurement were taken in millimeters. Since most of the skulls were laterally flattened, with distortion increasing towards the posterior region of the skull, landmarks were selected only in lateral view and anterior to the orbit. Severely fragmentary or distorted specimens were not included. Missing data were estimated with regressions, acknowledging the problems, such as an artificial shape uniformity, associated with such procedures (Dodson, 1975; Smith, 1998). Loss of data was concentrated in the nasal region (Table 1), normally associated with loss of the premaxilla in two small specimens and one large one. All three specimens exhibit a very typical shape pattern, otherwise. We assume bilateral symmetry. Additionally, the sample is assumed to be representative of the Ghost Ranch population.

All analyses were performed with SAS and Excel at the University of Arizona. Univariate, bivariate, and multivariate statistical techniques (Bookstein et al., 1985) were used to locate consistent variation within the sample. One analysis was performed using only complete specimens. Univariate size-frequency distributions were calculated for each of the measurements (Table 1). For such statistical analyses, the data are typically log-transformed for several reasons (Weishampel and Chapman, 1990). Heteroscedasticity is typically present in such analyses, so a log transformation tends to reduce its effects. The results of

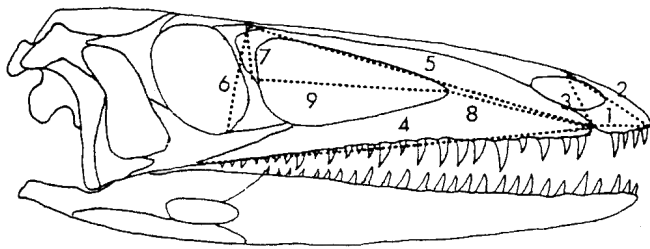


FIGURE 1. Skull of *Coelophysis bauri* in lateral view with landmarks indicated. (After Colbert, 1989).

TABLE 1. Univariate and bivariate statistics performed on twenty-three skulls using raw data. v1-v9 measurements (mm) correspond to Fig 1. Missing data were estimated. The percentages of missing data for each variable are indicated in the second column. s, estimated standard deviation; CV, coefficient of variation; $\hat{\alpha}$, estimated RMA slope; $\hat{\beta}$, estimated intercept; CI, 95% confidence interval. *Megapnosaurus (Syntarsus) kayentakatae* data were not included in these results. The variable lacking values represents the x-axis for the regressions.

Variable	% missing	Mean	Range	s	CV	α	β	CI(α)	CI(β)
v1	16	16.7	9-34.7	5.95	2.58	0.02	7.40	0-0.04	7.14-7.62
v2	20	25.7	9.5-52.3	9.69	1.88	0.05	6.53	0.03-0.07	5.83-7.23
v3	12	17	8.3-41	6.35	2.65	0.02	5.11	0-0.04	4.81-5.41
v4	4	99.8	37-175	43.51					
v5	0	89	34.3-175	42.89	8.61	0.97	-7.53	0.95-0.99	-23.23-6.17
v6	0	30.9	13-52	10.25	1.76	0.06	11.17	0.04-0.08	10.39-11.95
v7	8	14	6.1-26.4	6.09	3.72	0.02	5.29	0-0.04	5.01-5.57
v8	0	28.7	8.5-61.6	15.70	2.49	0.13	-4.01	0.11-0.15	-5.83-2.18
v9	0	57.8	15.9-105	26.52	1.62	0.37	1.21	0.35-0.39	-4.01-6.43

extracting the PCA from both covariance and correlation matrices from ln- and non-ln transformed data were compared. A total of four permutations were performed. Plots and results of the ln-transform extraction using a correlation matrix are presented here.

Bivariate regressions to describe allometric trajectories (Table 1) were calculated with a reduced major axis technique (R. Chapman, personal commun., 2006) using data from each of the individual variables with that variable, v4 (maxillary tooththrow length), loading most heavily on the first principal component (PC I), interpreted here as a size component (Rencher, 1995). A reduced major axis approach allows measurement error in both the x- and y-axes. Deviations from a single trend in such plots can reveal the presence of more than one taxon (Gould, 1966). Ninety-five percent confidence intervals were computed using the standard equations for the slope, $m + t_{\alpha/2}(s_e/(S_{xx})^{1/2})$ where $S_{xx} = \sum x^2 - (\sum x)^2/n$ and the intercept $b = t_{\alpha/2}(s_e/(S_{xx})^{1/2})$, where $s_e = (SSE/(n-2))^{1/2}$ and $SSE = \sum(y - \hat{y})^2 = \sum(y - \hat{y})^2 + \sum(\hat{y} - \bar{y})^2$ (Ott, 1993). Most of these terms were computed by SAS. For calculating the allometric trajectories of *Coelophysis bauri*, because much of this paper deals with variation in that taxon only, the *Megapnosaurus (Syntarsus) kayentakatae* data were deleted. Alternatively, regression plots were created with the *Coelophysis* data that compared those measurements that loaded least heavily on PC I. The three plots presented here include premaxilla height vs. lacrimal cavity, premaxilla length vs. lacrimal height, and lacrimal height vs. maxillary tooththrow length.

Principal Components Analysis (PCA) maximizes within-group variation of a single sample and is not sensitive to multivariate normality. Therefore, it is commonly used in such studies and the mechanics are described elsewhere (Rencher, 1995). Other assumptions and techniques were identical to those incorporated in a discussion of variation in *Allosaurus*. (Smith, 1998). In the case presented here, the eigenvectors (Table 2) were extracted from a correlation matrix. The *Megapnosaurus*

(*Syntarsus) kayentakatae* data were included in these analyses. Loading contrasts were used to uncover the relationships among the variables. Only those with relatively high absolute values were retained, while those close to zero were dropped. Meaningful principal components were taken as those whose loading interpretations made biological sense. Subsequent components were regarded as uninterpretable. Plots were created of PC I vs. PC II, PC I vs. PC III, and PC II vs. PC III.

RESULTS

There is a substantial amount of morphometric variation in this sample, with a significant amount a result of taphonomic distortion. The relatively low magnitude loadings on the first principal component support this conclusion. Despite this problem, a meaningful biological signal is still present. The size percentages of many of the univariate distributions are close to normal. Allometric trajectories, excluding *Megapnosaurus (Syntarsus)* were computed using the raw data (Table 1). Correlations varied from low to very high. In all cases, the 95% confidence interval excluded one, so isometry can be excluded as a hypothesis (Table 1), with the possible exception of the distance from the maxillary notch to the top of the lacrimal. These results should not be taken as implying that *Coelophysis* grew linearly, but that that part of the allometric trajectory represented by the available specimens could be explained by a straight line.

The bivariate plots of the ln-transformed data (Figs. 2A-C) also suggest the presence of a single, poorly defined trajectory. In plotting the lacrimal height against maxillary tooththrow length (Fig. 2A), a straight line explained the data. There may be some bimodality in the results. *Megapnosaurus (Syntarsus)* collapsed close to the general *Coelophysis* trend. When the premaxilla height is plotted against the lacrimal cavity, there is a considerable amount of individual variation observed within the general trend. These results suggest that the development of the lacrimal cavity is highly variable. Similar results regarding this structure were observed for *Allosaurus*. *Megapnosaurus (Syntarsus)* was close to the general trend. When premaxilla height was plotted against lacrimal height (Fig. 2C), very similar results were obtained, such that there was a single trend with considerable scatter.

Typically, the first principal component is interpreted as a size vector, especially if all of the loadings are strongly positive as they are in these results. PC I explains 77% of the observed variation (Table 2). Both the second and third components are contrasts describing the development of the antorbital fenestra (Table 2). This Principal Component explains another 9% of the observed variation. The third Principal Component is primarily a contrast between the length of the external nares and the antorbital fenestra. It explains 4% of the observed variation. The fourth principal component was not interpretable.

Plotting Principal Components I and II (Fig. 3A) reveals a single linear trend, presumably reflecting an ontogenetic trajectory. Two size-related clusters were observed, the smaller one with eight plotted specimens and the larger with 14. One *Coelophysis* specimen, AMNH 7227, plots close to *Megapnosaurus (Syntarsus) kayentakatae*. Both have deeper skulls relative to length than is normal for *Coelophysis*. AMNH 7227 (Fig. 4A) has an unusually short snout with a high cranial region (compare with Fig. 4B), similar to that of *Megapnosaurus (Syntarsus) kayentakatae*, but it lacks the diagnostic morphological characters for that species, such as a crest and a nasal fenestra (Rowe, 1989).

When the second Principal Component is plotted against the third (Fig. 3B), a single large, poorly-defined cluster with a number of outliers results. While much of the observed variation is probably a result of taphonomic distortion, *Megapnosaurus (Syntarsus) kayentakatae* is located far from this main group.

When the first Principal Component is plotted against the third (Fig. 3C), the two clusters previously observed are still present. *Megapnosaurus (Syntarsus)* is far from either cluster, but would be most closely associated with the largest class, but not as large as a large

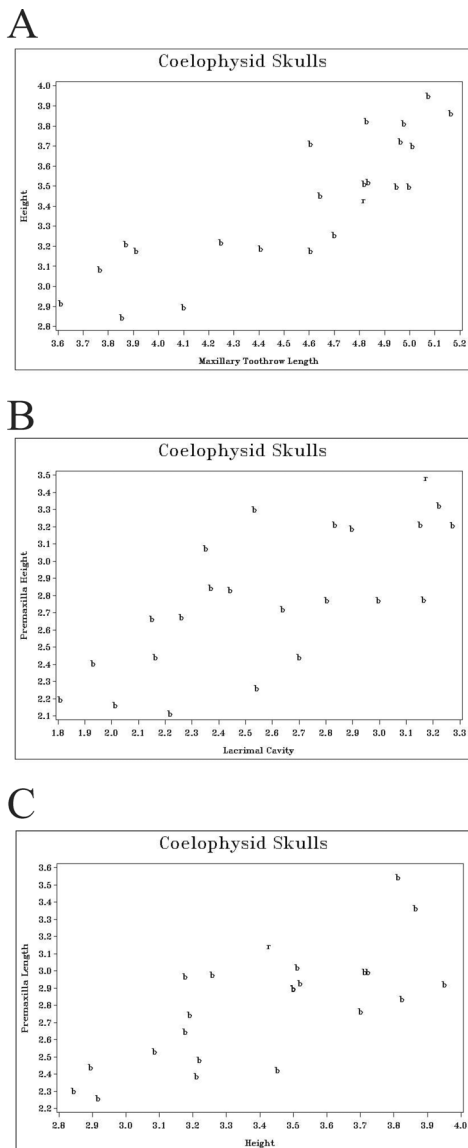


FIGURE 2. Bivariate plot of the *Coelophysis bauri* sample, with *Syntarsus kayentakatae* included, using ln-transformed data and a reduced major axis model to compute best-fit line. **A**, Regression equation is $V6 = 0.421V4 + 1.32$, $r = 0.71$. X-axis is the lacrimal height and Y-axis is the maxillary tooth row length. **B**, Regression equation is $V3 = 0.833V7 + 1.166$, $r = 0.56$. X-axis is the lacrimal cavity and Y-axis is the height of the premaxilla. **C**, Regression equation is $V9 = 0.99V7 + 0.26$, $r = 0.75$. X-axis is the lacrimal height and Y-axis is the length of the premaxilla. All measurements are in millimeters. b, *Coelophysis bauri*; r, *Syntarsus kayentakatae*.

Coelophysis.

DISCUSSION

A single ontogenetic trajectory of the sample from Ghost Ranch from juvenile to adult of a single theropod species is indicated by many, but not all, of these results. Age is regarded as correlated with size. Extremely small individuals are not present in the analysis. Some individual variation, like that seen in the skull of *Allosaurus fragilis* (Smith, 1998, 1999), was observed for *Coelophysis bauri*, but it remains to be seen if it is high compared to the postcranial skeleton. Variability increased with the size range of the specimens, indicating the presence of heteroscedasticity in the data set. There is, however, a biological signal present that reveals many of the expected allometric changes.

Most bivariate plots show a single, more or less well-defined,

TABLE 2. Principal Components extracted from a correlation matrix from twenty-three skulls of *Coelophysis bauri*. *Megapnosaurus* (*Syntarsus*) *kayentakatae* data are included in these results. These results explain 90% of the observed variation.

Variable	Eigenvectors		
	PC1	PC2	PC3
v1	0.308	0.309	0.646
v2	0.346	0.126	-0.479
v3	0.326	0.464	-0.283
v4	0.366	-0.214	-0.120
v5	0.338	-0.369	0.361
v6	0.347	-0.091	0.235
v7	0.297	0.421	-0.111
v8	0.314	-0.493	0.265
v9	0.351	-0.252	-0.071
Proportion	0.77	0.09	0.04

ontogenetic trajectory, supporting the common interpretation that most of the variation is a result of growth in one species. There is some indication of two size classes contained within the sample, but this bimodality is not as pronounced as that observed for *Allosaurus*. It may well reflect size-related sexual dimorphism present in the sample, with one sex being more common than the other. As in *Allosaurus*, many of the extra-cranial bones of the skull are expected to show more individual variation than any other bones in the skeleton (Smith, 1999). The interpretation of the multivariate analyses supports the hypothesis that much of the observed variation results from a combination of sexual variation combined with taphonomic distortion. Additionally, *Megapnosaurus* (*Syntarsus*) is distinct from *Coelophysis*. Overall, *Coelophysis bauri* typically has a long, low skull compared to *Megapnosaurus* (*Syntarsus*) *rhodesiensis* and *M. (S.) kayentakatae* at any stage of growth.

Like *Allosaurus*, statistical plots indicate the presence of a bimodal, size-related distribution along a single allometric trajectory that may be related to sexual dimorphism within a single species (Smith, 1998), but the pattern is much weaker than that observed for that genus. The relationship, if any, of these clusters to postcranial differences previously described (Colbert, 1990), has not yet been analyzed.

The development of a crest is subtle, if present at all. The interpretation of its existence is highly confounded by taphonomic distortion present to varying degrees in all of the skulls. It seems that it will be difficult, therefore, to subdivide the *Coelophysis* sample based on this character alone. However, clarification of this issue awaits a forthcoming morphological description of the *Coelophysis* skull (R. Sullivan, personal commun., 1997).

Coelophysis bauri is closely related to the Early Jurassic theropods *Megapnosaurus* (*Syntarsus*) *rhodesiensis* and *M. (S.) kayentakatae* (Holtz, 1998) from Zimbabwe and Arizona, respectively. The morphology of the two supports this model, as differences tend to be subtle. In his dissertation, Raath (1977) summarized some apparent differences between the two taxa. They include differences in the skull height/length ratio, differences in the form of the basisphenoid, the presence/absence

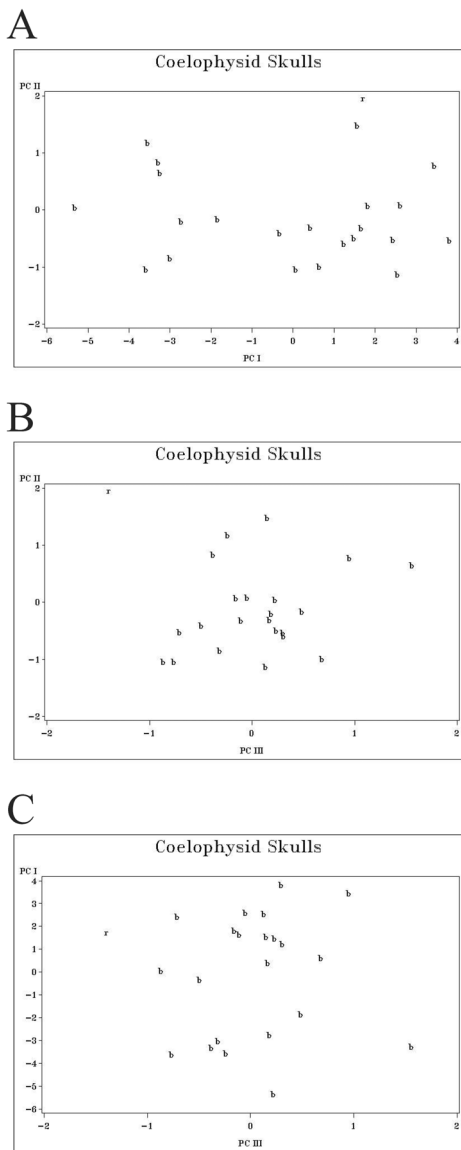


FIGURE 3. Plots of Principal Components Analyses using ln-transformed data. **A**, Plot of PC I vs. PC II extracted from a correlation matrix. **B**, Plot of PC II vs. PC III extracted from a correlation matrix. **C**, Plot of PC I vs. PC III extracted from a correlation matrix. b, *Coelophysis bauri*; r, *Syntarsus kayentakatae*.

of a nasal fenestra, the relative length of the antorbital fenestra, the relationship of the lacrimal to the jugal, and the degree of fusion of the proximal ends of metatarsals II and III. Rowe (1989) noted that at least two of these characters, the nasal fenestra and increased metatarsal fusion, may have been present in *Megapnosaurus (Syntarsus) kayentakatae*. However, Bristowe and Rowe (2004) reinterpreted that region such that there was, in fact, no nasal fenestra in *M. (S.) rhodesiensis*. Some distinguishing characters between *Coelophysis bauri* and *Megapnosaurus (Syntarsus) rhodesiensis* noted by Colbert (1989) include differences in the extension of the tooth row and maxillary tooth counts. With few exceptions, Bristowe and Raath (2004) discounted most of the other morphological differences. *M. (S.) kayentakatae* can still be distinguished from most specimens of *Coelophysis bauri*, except for AMNH 7227, on the basis of the relatively high skull dimensions. The results presented here indicate that this specimen should be re-examined for morphological characters specific to *Megapnosaurus (Syntarsus)*.

Of these characters, some require further discussion. As also noted by Bristowe and Raath (2004), the lacrimal does not actually laterally

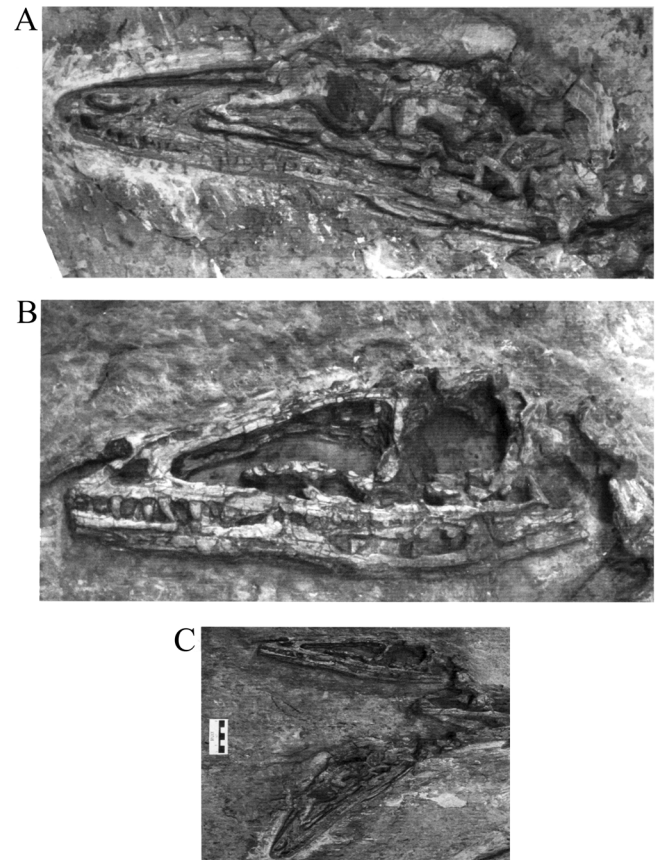


FIGURE 4. *Coelophysis bauri* skulls in lateral view. **A**, AMNH 7228, and **B**, AMNH 7227. **C**, Both are on the same bedding plane and block (AMNH Block IX). AMNH 7228 is more typical of overall *Coelophysis bauri* morphology.

overlap the jugal in *Megapnosaurus (Syntarsus) rhodesiensis* (also noted by Tykoski, 1998), which would be a highly unusual condition. Another character, the difference in the relative length of the antorbital fenestra to total skull length may be misleading. Colbert regards the ratio of 0.33 as important in distinguishing the two taxa. The antorbital fenestra of *Megapnosaurus (Syntarsus) rhodesiensis* is greater than 0.33, *Coelophysis bauri*, less. Rowe (1989) used a value of 0.40 to distinguish the two.

In the current study, many of the *Coelophysis bauri* skulls were severely deformed posteriorly. Therefore, the total tooth row length from the tip of the premaxilla to the end of the maxilla ($v1 + v2$) was used as a proxy for total skull length. The length of the antorbital fenestra was then divided by this value. The range in values obtained by this method for *Coelophysis bauri* was 0.31 to 0.71. The mean value was 0.49 and the standard deviation was 0.9. The ratio for *Megapnosaurus (Syntarsus) kayentakatae* was 0.39. Therefore, the value for *M. (S.) kayentakatae* was about one standard deviation from the mean of *Coelophysis* and well within the range of the latter. In hindsight, such a result might not be unexpected, since the facial region of the skull is the most variable region of the skeleton (Smith, 1998). Extending from these results, caution should be used in using such ratios in this part of the skull to diagnose taxa.

The difference in skull height versus length was detected using morphometric methods in the current study, as well as by Raath (1977). It is unclear why this character, among others, was not published in later summaries (D. Chure, personal commun., 2001). Given a shorter skull length and similar sized teeth, it might be expected that tooth counts (Colbert, 1989) for *Megapnosaurus (Syntarsus) rhodesiensis* (19-20) would be lower than in *Coelophysis bauri* (22-26). Photographs of the

two taxa (Colbert, 1989; Rowe, 1989) indicate that the maxillary tooth rows end beneath the orbit in both rather than ending under the lacrimal as suggested by Colbert (1989)

The results presented here do not support the contention that *Megapnosaurus* (*Syntarsus*) was present at the Ghost Ranch Quarry and further that *Megapnosaurus* (*Syntarsus*) cannot be synonymized with *Coelophysis*. Typically, *Coelophysis bauri* has a long low skull at any stage of growth, but a skull removed from the general ontogenetic trend, broadly similar to one specimen of *Coelophysis*, AMNH 7227, is shorter and deeper compared to other *Coelophysis* specimens and may warrant further study. Specimens from lower in the section at Orphan Mesa are apparently significantly different morphologically from the Ghost Ranch material (Sullivan and Lucas, 1999). This material has not been included in these analyses due to their incomplete nature.

It is thus more parsimonious, the lack of morphological or statistical data to the contrary, to posit the existence of only one coelophysid species in the Ghost Ranch Quarry. The taxonomy of Colbert (1989) and Colbert et al. (1992) is followed in ascribing the name *Coelophysis bauri* to all of the theropod material found to date from this site. The allocation of *Coelophysis* to the Podokesauridae, however, has not been adequately substantiated and the latter probably does not represent a holophyletic clade. Therefore, its inclusion in a separate Coelophysidae, following Paul (1993) and Holtz (2000) is supported.

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