MORPHOMETRIC ANALYSIS OF THE FORELIMB AND PECTORAL GIRDLE OF THE CRETACEOUS ORNITHOPOD DINOSAUR *ORYCTODROMEUS CUBICULARIS* AND IMPLICATIONS FOR DIGGING

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ABSTRACT—The basal ornithopod *Oryctodromeus cubicularis* was described as burrowing due to its discovery in a burrow structure, and the presence of several morphological features considered consistent with burrowing. Using traditional and geometric morphometric analyses, the morphology of the humerus and scapula of ornithopods, basal ornithischians, and marginocephalians was analyzed to describe and characterize quantitatively the differences between *Oryctodromeus* and other ornithopods. These differences were then compared with the morphological adaptations for digging in mammals, because there are no adequate analogues for burrowing in extant archosaurs. A canonical variates analysis was also conducted on the geometric morphometric data to determine if phylogeny impacted morphological trends. The humerus of *Oryctodromeus* is slightly more robust than other basal ornithopods, indicating an adaptation for increased force applied to the humerus. The scapula provides the most compelling morphological support for digging in *Oryctodromeus*. The large acromion process and prominent scapular spine of *Oryctodromeus*, as well as the large posterovertrally expanded scapular blade, distinguish the scapula of *Oryctodromeus* from those of other ornithopods and would have provided surface areas for the attachment of the supracoracoideus, deltoideus clavicularis, and deltoideus scapularis muscles, the latter of which is important in digging in mammals. These features provide evidence for specialization for producing burrows by scratch digging.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Digging is a behavior that has only recently been explored in dinosaurs (Bakker, 1996; Senter, 2005, 2007; Varricchio et al., 2007; Martin, 2009; Sereno, 2010; Simpson et al., 2010; Fowler and Hall, 2011; Huh et al., 2011). For example, the basal ornithopod *Oryctodromeus cubicularis* was described as potentially constructing burrows with its forelimbs due to its discovery in a burrow structure and morphological features potentially advantageous for digging, such as expanded and fused premaxillae, an expanded sacrum and a greater attachment area between the pelvis and sacrum relative to other basal ornithopods, and a robust, fused scapulocoracoid with a prominent scapular spine (Varricchio et al., 2007). An actualistic taphonomic study tested whether the patterns of infilling and disarticulation seen in the burrow structure were parsimonious with the hypothesis that the specimens of *Oryctodromeus* died within the burrow structure and were disarticulated and buried by later infilling of the burrow. The study found that the state of disarticulation of specimens of *Oryctodromeus* was possible for organisms already present in the burrow, and that the bones were unlikely to have been washed into the burrow after disarticulation (Woodruff and Varricchio, 2011).

The only other dinosaurs described as burrowing have been basal ornithopods, namely, *Drinker* (Bakker, 1996) and *Koreanosaurus* (Huh et al., 2011). Although the phylogenetic position of *Drinker* is not well known, the presence of diagnostic characteristics in *Koreanosaurus* led to its placement in a monophyletic clade that includes *Oryctodromeus*, *Orodromeus*, and *Zephyrosaurus* (Varricchio et al., 2007; Huh et al., 2011). Boyd et al. (2009) found that *Thescelosaurus* also belonged to this clade, but Butler et al. (2008) described *Thescelosaurus* as more derived than *Hypsilophodon*. Basal ornithopods are all small—up to 4 m in *Thescelosaurus*, the largest basal ornithopod (Boyd et al., 2009)—and, with the exception of *Koreanosaurus*, bipedal. Ornithopods are relatively morphologically conservative. However, body size and locomotor style vary across the entire clade (Fig. 1), with basal ornithopods having a typically bipedal gait and small body size and more derived ornithopods having a quadrupedal gait and larger body size (Fastovsky and Weishampel, 2005). The changes in body size and locomotion that trend with phylogeny may also cause a trend in morphology. Iguanodontians have an intermediate morphology, with a large range in body size. Humeral morphology appears more similar to basal ornithopods, whereas scapular morphology more closely compares to hadrosaurids (Norman, 2004). Iguanodontian locomotion varies with age and body size, typically juvenile and smaller iguanodontians are considered bipedal, whereas adult iguanodontians are considered facultatively bipedal to quadrupedal (Norman, 2004). Hadrosaurids are the most derived ornithopods, and all share large body size and facultative bipedal to quadrupedal gait (Horner et al., 2004). Although burrowing behavior is present in birds and crocodilians, such as burrowing owls (Thomsen, 1971), Magellanic penguins (Stokes and Boersma, 1991), blue penguins (Waas, 1990), bank swallows (Bent, 1942), kingfishers (Skutch, 1957), American alligators (Martin et al., 2012), and Chinese alligators (Chu,
because the morphologies of the forelimb elements vary so dig-
ing in mammals might be appropriate analogues. However, Meus
does not provide a suitable framework for analyzing dig-
tions from several sources (Scheetz, 1999; Varricchio et al., 2007;
and hind limbs to excavate rather than their forelimbs, whereas
crocodylians dig with both hind limbs and forelimbs, but lack any
morphological specializations for digging (Kley and Kearney,
2007). The osteological correlates of burrowing in mammals,
however, have not been analyzed phylogenetically and are therefore shown in a
polytomy with other iguanodontians. This tree was compiled using rela-
tionships from several sources (Scheetz, 1999; Varricchio et al., 2007;
Butler et al., 2008; fig. 4; McDonald et al., 2010; Makovicky et al., 2011).

MATERIALS AND METHODS

A morphometric analysis allows for quantitative descriptions and morphological comparisons between different specimens or species (Zelditch et al., 2012). In traditional morphometrics, a series of measurements used as descriptors of shape are compared. However, this method can lead to a loss of overall shape information due to the constraints of straight-line measurements and the inability to account for how each measurement relates to another spatially (Zelditch et al., 2012). In geometric morphometrics, landmarks representing homologous structures or inflec-
tion points on elements and semilandmarks representing non-
homologous points that usually describe the curvature of an ele-
ment are superimposed on photographs of elements in order to
compare shapes of different specimens (Zelditch et al., 2012).

Although this method gives an overall better description of shape than traditional morphometrics, geometric morphometrics can result in a loss of information due to the two-dimensional nature of the method (Zelditch et al., 2012). Both traditional and geometric morphometric analyses were run to more thoroughly describe the forelimb morphologies of several ornithis-
chian taxa.

A total of 73 humeri and 47 scapulae from 18 genera of ornithis-
chian dinosaurs were measured and photographed for the tradi-
tional and geometric morphometric analyses (Fig. 1), including 12 humeri and four scapulae from smaller, potentially juvenile specimens (see Supplementary Data). Length measurements of morphological features were used in the traditional morphometric analysis, and morphological landmarks were digitized from photographs for the geometric morphometric analysis. For sim-
licity of description, the scapula is described not in life position, but with the scapular blade in a horizontal orientation. Unlike a phylogenetic analysis, neither traditional nor geometric
Traditional Morphometric Analysis

For the traditional morphometric analysis, 10 measurements were taken on the humerus and nine on the scapula (Table 1; Fig. 2). Due to the availability of complete specimens, taxonomic representation varied between elements with 18 and 17 genera, respectively. The samples for each also included specimens not identified beyond family or subfamily (Appendix 1). Some of the following measurements were modified from and expanded upon Galton’s (1974) description of Hypsilophodon. Measurements greater than 150 mm were taken with a flexible tape measure; measurements less than 150 mm were taken with General UltraTECH calipers.

Measurements were chosen to describe the maximal shape variation between the different genera to provide the most informative results. However, it is difficult to describe all shape variation via linear measurements; certain morphological data are lost, for example, in the humerus, the orientation of the deltopectoral crest relative to the orientation of the proximal end. In basal ornithopods, the deltopectoral crest expands perpendicular to the proximal humerus, whereas in more derived ornithopods and hadrosaurs, the deltopectoral crest is more in line with the orientation of the proximal humerus. As also illustrated by the humerus, phylogenetic differences make certain measurements more difficult to ascertain in certain groups. More derived ornithopods have a reduced acromion process and less concavity to the proximal scapula, making discernment of the scapular spine length difficult in certain specimens.

After the measurements were compiled, the data were analyzed using principal components analysis (PCA) in the statistical analysis program R (version 2.11.1; R Development Core Team, 2010). Principal components analyses can describe the variance between different specimens and how different aspects of the shape of an element vary between specimens. In traditional morphometrics, PCA is an ordination method that reduces the number of variables to work with by generating a few significant principal components, which are linear combinations of the measurement variables (Hammer and Harper, 2005). As per common convention, principal components are considered significant if the eigenvalue is greater than 1 (Manly, 2005). Data standardization so that each measurement has an equal mean yields the variance-covariance matrix, and standardization that produces equal means and variances for each measurement yields the correlation matrix. The PCA can then be run on either the variance-covariance matrix or the correlation matrix, although the latter is preferred and was used in this analysis (Manly, 2005). The values along the diagonal of the variance-covariance matrix represent the variance of each observation, and the sum of the variance is equivalent to the sum of the eigenvalues, which represent the variance of the principal components. Therefore, the amount of variation described by the raw data and the principal components remains constant (Manly, 2005). Often, when comparing objects of varying sizes, the first principal component is a descriptor of size and may account for a large portion of the variance (Manly, 2005). In order to minimize the impact of size, some studies have used femur shaft diameter as a proxy for body size (Maloit et al., 1979; Kambic, 2008). Due to a lack of associated femoral material for many specimens in this study, the body size of each specimen could not be accounted for. However, element length was accounted for by dividing all other variables by total element length, so that the shape could be analyzed as a ratio of each measurement against size. Therefore, it is important to note that a ratio does not

![Table 1](https://www.example.com/table1.png)

Refer to Figure 2 for illustrations of these measurements.
remove the confounding variable of body size in the analysis, but instead reduces the variance directly explained by size so that shape information can be analyzed (Corruccini, 1987). The measurements as ratios to element length are denoted by an ‘r’ subscript. To test for a direct correlation between morphological variation and size, PC scores of significant axes were regressed against element size.

**Geometric Morphometric Analysis**

Geometric morphometric analyses use the relative positions of morphological landmarks and semilandmarks on an element to mathematically describe the differences between specimens (Zelditch et al., 2012). This generates a more comprehensive description of shape than only length and width measurements can provide. Landmarks defined by homologous points are considered the most reliable frames of reference in morphometrics. Because homology is difficult to define in fossil taxa and is rarely limited to a definable point, corresponding structures are used instead. Corresponding structures are not necessarily developmentally homologous, but are functionally and anatomically similar (Zelditch et al., 2012). However, in some cases corresponding structures cannot be defined; therefore, points of maximum curvature are used. Semilandmarks are used to describe the shape of a curve and are weighted to prevent semilandmark data from obscuring data from true landmarks (Zelditch et al., 2012).

For the geometric morphometric analysis, landmarks and semilandmarks were superimposed on photographs of each element in a specific orientation so that the points would be comparable between specimens (Zelditch et al., 2012). Scapulae were photographed in lateral view with the blades oriented horizontally, and humeri were photographed in anterior view. Using the Thin Plate Spline (TPS) suite of computer programs, these photographs were converted to a TPS file with TPS Utility Program (Rohlf, 2010a), then imported into TPSDig2 (Rohlf, 2010b), where scale and landmark data were superimposed on the photographs.

For the humerus, eight landmarks and 10 semilandmarks were used in the analysis (Table 2; Fig. 3). This study includes 58 specimens from 18 distinct genera and 12 specimens not identified beyond family or subfamily level. Seven of the landmarks were inflection points rather than corresponding structures, because it is difficult to locate homologous points on the humerus. The only landmark based on a corresponding structure is the apex of the deltopectoral crest. The semilandmarks are used to describe the overall shape of the humeral shaft (Fig. 3), with five semilandmarks equally spaced following the curves between the medial epicondyle landmark (8) and the medial end of the proximal humerus (1) and five semilandmarks equally spaced between the lateral epicondyle landmark (4) and the lateral edge of the proximal humerus (2).

### TABLE 2. Descriptions of the landmark positions on the humerus and scapula used in the geometric morphometric analysis.

| Landmark | Description                                      |
|----------|--------------------------------------------------|
| Humerus  |                                                  |
| 1        | Medial edge of the proximal humerus               |
| 2        | Lateral edge of the proximal humerus              |
| 3        | Apex of the deltopectoral crest                   |
| 4        | Inflection point of the lateral epicondyle        |
| 5        | Distal-most radial condyle                       |
| 6        | Inflection point of the intercondylar groove      |
| 7        | Distal-most ulnar condyle                        |
| 8        | Inflection point of the medial epicondyle         |
| Scapula  |                                                  |
| 1        | Dorsal end of the scapulocoracoid suture          |
| 2        | Dorsal end of the scapular spine                  |
| 3        | Posterior inflection of the acromion              |
| 4        | Superior angle                                    |
| 5        | Inferior angle                                    |
| 6        | Ventral edge of the scapular glenoid              |
| 7        | Ventral edge of the scapulocoracoid suture        |
| 8        | Posterior margin of the deltoid fossa where the   |
|           |  glenoid ridge meets the scapular spine           |

Refer to Figure 3 for illustrations of these landmarks.
A total of 37 scapulae from 16 distinct genera, as well as three specimens not identified beyond family or subfamily level, were used in the geometric morphometric analysis. In the scapula, there are eight landmarks and 15 semilandmarks (Table 2; Fig. 3). Four of the landmarks are corresponding structures (points 1, 2, 6, and 7); the remaining four are inflection points. The semilandmarks describe the shape of the scapular blade. Five semilandmarks evenly spaced between the posterior inflection of the acromion (3) and the superior angle (4) describe the dorsal margin of the blade, five semilandmarks spaced evenly between the superior angle (4) and the inferior angle (5) describe the posterior margin of the blade, and five semilandmarks spaced evenly between the inferior angle (5) and the ventral-most edge of the scapular glenoid (6) describe the ventral margin of the scapular blade.

The landmarks were mathematically described by conducting a relative warp analysis (RWA) using TPS Relative Warps (Rohlf, 2010c), to calculate the relative warp scores. The TPS file and relative warp scores were then converted to procrustes distances in the Integrated Morphometrics Package (IMP) program CoordGen6h (Sheets, 2000). By using procrustes superimposition, the variation between specimens due to the orientation, size, and position of the elements in the photograph can be removed by normalizing the photographs so that each element has an equal centroid size, and then arranging points around the centroid of the element. This causes the influence of shape on the arrangement of points to become more evident. Although RWA and PCA are very similar, the axes of an RWA may be weighted by the bending energy of the warp. When the axes of a RWA are not weighted, the results of an RWA are equivalent to a PCA (Zelditch et al., 2012). As in the traditional morphometric analysis, the RWA scores were regressed against element size to test for any correlation that would explain the variation in shape.

Canonical variates analyses (CVA), a type of discriminant function analysis (DFA), were also run on these data to compare the morphological data with discrete phylogenetic groupings using the IMP program CVAGEN6o (Sheets, 2006). DFA tests whether morphology can be used predictively to determine classification into a group. DFA does this by generating canonical variates that minimize within-group variation and maximize between-group variation (Zelditch et al., 2012). Like PCA, CVA is an ordination method that reduces the number of explanatory variables describing the variation between groups to a more manageable number of axes (Manly, 2005). CVA was used in this study to determine if the variation in morphology between phylogenetic groups truly followed phylogenetic trends.

The phylogenetic groupings evaluated were basal ornithischians, basal ornithopods, iguanodontians, hadrosaurids, and marginocephalians. The classification of each taxon is based on the strict consensus tree in Butler et al. (2008:fig. 4; specific designations of each taxon are in Appendix 1). Most of these groups are grades rather than monophyletic clades, with much instability in the position of some taxa. Similarly, there is an evolutionary relationship between some grades, such as basal ornithopods and iguanodontians, causing designation of the most derived basal ornithopods or least derived iguanodontian to fluctuate between different studies and different analysis methods.

RESULTS

Traditional Morphometrics

The results for the PCA on the correlation matrix of the raw measurement data (see Supplementary Data) for the humerus and scapula indicate that most of the variance is due to the overall size of the element, rather than difference in shape. In the humerus, the first principal component (PC1) describes 94.9% of the variation in the data, and PC2 describes 1.8% of the variation, and is insignificant. All other principal components are insignificant for both the humerus and the scapula. Due to a general trend of increasing size across ornithopod phylogeny, this yields a trend of basal ornithischians and basal ornithopods having low PC1 scores, and adult hadrosaurids with high PC1 scores. Because these results correlate with size (for the humerus, $R^2 = 0.975$; for the scapula, $R^2 = 0.981$), they do not give any shape information and will be disregarded from further discussion.

Humerus—In the humerus, when all other variables are divided by total humeral length and the data analysis computed as ratios, influence of shape rather than size on the variation between specimens becomes more apparent (Fig. 4). The first three principal components of the correlation matrix together describe 71.2% of the variation (PC1 explains 37.9%, PC2 explains 19.4%, PC3 explains 13.8%); the remaining six principal components are insignificant, as the eigenvalues are less than 1. PC3 exhibits the most separation between different groups (Fig. 4C).

The weightings of PC1 indicate that it is primarily impacted by a positive correlation of all of the variables, with the most weight due to the longer measurements: the ratio of the deltopectoral crest length to humeral length (DPLr) and the ratio of distal humeral width to humeral length (HDWr). Basal ornithopod humeri produce more positive PC1 values and hadrosaurids typically have negative PC1 values; iguanodontians exhibit a large range of PC1 scores encompassing the entire range of basal ornithopods and hadrosaurids. This weak separation roughly follows phylogeny and increasing adult body size and change in locomotor style from bipedal to quadrupedal, although there is a large degree of overlap between the groups. However, basal ornithischians and marginocephalians are not morphological outliers as one would expect if PC1 were explained primarily by phylogeny or body size, but instead group with basal ornithopods and hadrosaurids, respectively. Specimens of Oryctodromeus have the most strongly positive PC1 scores, but do not appear to be significantly different from other basal ornithopods. PC1 does
not have functional significance in relation to digging and instead appears to trend with size and locomotor style, with small bipedal basal ornithopods with positive scores and large quadrupedal derived ornithopods with negative scores. Regressing PC1 scores against humeral length (as a proxy for body size) yields no support for a direct linear correlation between PC1 and size, even after removing juvenile specimens from the analysis ($R^2 = 0.212$). Like size, which superficially appears to trend with PC1, locomotor style also appears to trend with PC1, where quadrupedal ornithischians such as hadrosaurids and iguanodontians have smaller PC1 values, and bipedal basal ornithischians and basal ornithopods have larger PC1 values. However, some basal iguanodontians seem to be an exception to this, because they are considered quadrupedal but have large PC1 scores. For example, *Camptosaurus* is suggested to be quadrupedal based on manus morphology, without significant specialization of the humerus or scapula (Carpenter and Wilson, 2008).

The second principal component is controlled by deltopectoral width (DPW$_r$), humeral proximal width (HPW$_r$), and humeral distal width (HDW$_r$) versus radial condyle width (RCW$_r$) and ulnar condyle width (UCW$_r$), all relative to humeral length, describing the relative robustness of the humerus, especially at the ends. A more positive value indicates narrow proximal and distal ends and a narrower deltopectoral crest and/or distal condyles that are dorsoventrally expanded, whereas more negative values indicate wider proximal and distal ends with a more robust deltopectoral crest and/or shorter distal condyles. This component is not influenced by phylogeny, because basal ornithopods, iguanodontians, and hadrosaurids all occupy roughly the same range of PC2 values. There is no support for a linear correlation of PC2 and body size ($R^2 = 0.0401$). There does not appear to be any discernible functional trend in PC2. Both *Hypsilophodon* and *Dryosaurus* exhibit a wide range of PC2 scores, which show no linear correlation with humeral length ($R^2 = 0.1167$ and $R^2 = 0.1761$, respectively), indicating that the variety in scores is not likely due to ontogenetic change. The positive correlation with measurements in one plane and negative correlation with measurements in the perpendicular plane with no influence from measurements on the long axis of the humerus indicate that PC2 may have been partially influenced by the taphonomic deformation, because some of the more strongly positive and negative PC2 scores corresponded with specimens showing deformation.

Component three is explained primarily by DPL$_r$ and humeral shaft width anteroposteriorly (HSP$_r$) versus humeral head width (HHW$_r$) and RCW$_r$. A positive PC3 value indicates a longer deltopectoral crest relative to humeral length, a thicker humeral shaft, and a narrower humeral head and radial condyle, whereas a negative value indicates a relatively shorter deltopectoral crest and narrower shaft, with a relatively wider humeral head and radial condyle. Although there is large overlap between iguanodontians and basal ornithopods, there are few overlapping values between hadrosaurids and iguanodontians and between basal ornithopods and *Oryctodromeus*. This component appears to have significance outside of phylogenetic relationship or size.

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FIGURE 4. Traditional morphometric PCA results for the humerus. A, PC1 vs. PC2; B, PC2 vs. PC3; C, PC1 vs. PC3. Components one and two do not show any separation between *Oryctodromeus* and other basal ornithopods. However, in PC3, three of the four specimens of *Oryctodromeus* have positive scores whereas other basal ornithopods have negative scores, indicating a slightly more robust humerus in most specimens of *Oryctodromeus*. Specimens: a, *Oryctodromeus* (MOR 1636a); b–e, *Oro-

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dromeus* (MOR 623, MOR 294, MOR 404, MOR 473); f–h, *Hypsilophodon*

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(NHMUK R196, NHMUK R192, NHMUK R5830); k, *Thescelosaurus* (CM 9900); n and q, *Dryosaurus* (CM 21786, BYU 5215); s, Iguanodontian indet. (DBDP-42).
Oryctodromeus does not group with other basal ornithopods, and basal ornithischians do not have strongly positive scores as would be expected. Marginocephalians share PC1 ranges with iguanodontians and hadrosaurs, with the more quadrupedal Protoceratops scoring more strongly negative than the more bipedal Psittacosaurus. As is seen in the marginocephalians, PC1 scores may also roughly trend with locomotor mode, with quadrupedal ornithischians exhibiting negative PC1 scores and bipedal ornithischians with more positive PC1 scores.

The second component is influenced strongly by BLr, and IALr, and weakly by SAWr and SCALr. Longer scapular blades relative to the total length of the scapula would result in strongly positive PC2 values, whereas shorter blades relative to total scapular length would yield smaller or negative PC2 values. However, it appears that when looking at the specimens relative to the graph, an overall gross morphological trend is difficult to discern, nor does PC2 trend with phylogeny. It also shows no correlation with body size, even when juvenile specimens are removed ($R^2 = 0.0158$).

**Geometric Morphometrics**

**Humerus**—The geometric morphometric analysis of the humerus indicates that only the first two relative warp axes (RWA) are significant, together explaining 77.01% of the variation in shape (Fig. 6A). The RWA of the humerus indicates that basal ornithopods, iguanodontians, and hadrosaurs roughly separate out from one another, although there is considerable overlap between groups, especially with iguanodontians. When the relative warp axes are regressed against centroid size of the humerus, 85.4% of the shape variation remains unexplained, indicating that shape and size of the humerus (which is used roughly to estimate relative body size) are not linearly correlated.

The first relative warp (RW1) accounts for 60.27% of the shape variation and explains variation as the positive correlation between deltopectoral crest length and lateral offset of the deltopectoral crest. A positive RW1 represents a long deltopectoral crest with large lateral offset, such as in hadrosaurs. As in the traditional morphometric analysis, the humeri of Oryctodromeus have RW1 scores consistent with other basal ornithopods, although as end members of the variation within basal ornithopods, opposite more derived ornithopods. Marginocephalians exhibit a large difference in RW1 scores between the positive scoring Protoceratops (CM 9185) and the negative scoring Psittacosaurus (UoC LHVP2) due to the difference in deltopectoral crest length. Basal ornithischians exhibit similar scores to basal ornithopods, falling entirely within the same RW1 range.

The second relative warp (RW2) accounts for 16.74% of the variation and results from an inverse correlation between the length and the lateral offset of the deltopectoral crest. A positive RW2 score represents a short crest with large lateral offset, whereas a negative score indicates a longer deltopectoral crest with a smaller lateral offset from the humeral shaft. However, this may not accurately describe the variation in deltopectoral crest morphology due to the projection of three-dimensional objects into a two-dimensional analysis. In some specimens, particularly basal ornithopods, the deltopectoral crest expands anteriorly rather than laterally, and this shape information is lost in the reduction of dimensionality. In some hadrosaurs, the deltopectoral crest extends anterolaterally, so the true size of the deltopectoral crest is not represented by RW2. Specimens of Oryctodromeus have moderate RW2 scores, with relatively short deltopectoral crests with little lateral offset of the deltopectoral crest. Unlike RW1, in which specimens fall out roughly by their phylogenetic group, RW2 does not show a phylogenetic signal.

The canonical variates analysis indicated that there were three significant canonical variate axes (for CV1, $p = 9.14 \times 10^{-16}$; for CV2, $p = 0.00015$; for CV3, $p = 0.0118$). A plot of CV1 vs. CV2
shows the relative morphological separation of the different groups of specimens (Fig. 7A). The CV1 separates groups based on the length of the deltopectoral crest relative to humeral length, with more negative scores indicating a shorter deltopectoral crest relative to humeral length. The CV2 separated groups based on the width of the distal humerus and the orientation of the deltopectoral crest, with negative CV2 scores indicating a more laterally oriented deltopectoral crest and wider distal humerus. The CV3 separated groups based on the width of the distal and proximal humerus and deltopectoral crest length, with negative values having a narrower proximal and distal humerus and shorter deltopectoral crest length. Overall, there is a rough trend of CV1 with phylogeny among basal ornithopods, iguanodontians, and hadrosaurs, although *Oryctodromeus* does not follow this trend. Basal ornithischians and marginocephalians have scores similar to basal ornithopods and iguanodontians. Canonical variate two does not show any phylogenetic trend, with all ornithopods except *Oryctodromeus* scoring similarly, while CV3 shows a slight separation of basal ornithopods, including *Oryctodromeus*, from the more derived iguanodontians and hadrosaurs.

Specimens of *Oryctodromeus* grouped separately from other basal ornithopods in CV1 and CV2. To test the stability of the groupings, the specimens were a posteriori sorted into groups based on the canonical variates, and only seven specimens were incorrectly sorted: one iguanodontian was sorted as a basal ornithopod, five iguanodontians were sorted as basal ornithischian, and one basal ornithischian was classified as an iguanodontian. The uncertainty revolving around basal ornithischians may be due to the small sample size of the group, making it difficult to clearly define the morphology of the group.

As in the traditional morphometrics, the geometric morphometric analysis of the humerus indicates that the humeral morphology of *Oryctodromeus* is not significantly different from other basal ornithopods, although *Oryctodromeus* trends toward the more strongly negative extent of the range of PC1 scores of basal ornithopods. However, a different pattern arises when specimens are examined as groups in the CVA, indicating that overall *Oryctodromeus* does differ from other basal ornithopods in that it has more medially placed, anteriorly projecting, and relatively longer deltopectoral crest.

**FIGURE 6.** The first two relative warp axes from the RWA of the humerus and scapula. **A**, RWA of the humerus; **B**, RWA of the scapula; **C**, select humeri with varying morphologies; **D**, select scapulae with varying morphologies. The humerus shows a trend of larger, quadrupedal, derived ornithopods on the right, and small, basal, bipedal ornithopods on the left. Specimens of *Oryctodromeus* group with other basal ornithopods. The scapula exhibits a trend of larger, quadrupedal, derived ornithopods on the left, and basal ornithopods on the right. The scapular morphology of *Oryctodromeus* is distinct from other basal ornithopods, with strongly positive scores. Specimens: **a**, *Oryctodromeus* (MOR 1636a); **b–e**, *Orodromeus* (MOR 623, MOR 294, MOR 404, MOR 473); **f**, *Hypsipholodon* (NHMUK R196); **i**, *Haya* (FMNH IGM 100/2015); **k–l**, *Thescelosaurus* (CM 9900, MOR HC-164); **m**, *Tenontosaurus* (MOR 682); **n–p**, *Dryosaurus* (CM 21786, CM 3392, YPM 1876); **r**, *Iguanodon* (NHMUK R2196); **t**, *Maiasaura* (MOR 547a); **u**, hadrosaur indet. (CM 1066).
Scapula—The geometric morphometric analysis of the scapula indicates that RW1 and RW2 are the only significant axes, explaining 70.89% of the shape variation. The plot of RW1 vs. RW2 (Fig. 6B) shows that scapular morphology of ornithopods separates out phylogenetically, although there is some overlap in iguanodontian morphology and basal ornithopod morphology. However, the most striking aspect of the plot is the extreme separation of *Oryctodromeus* from the other taxa, showing a highly disparate morphology. Although the graph does appear to follow phylogenetic, size, and locomotor trends along RW1, when RW scores were regressed against centroid size of the humerus, 72.8% of the variation remained unexplained, indicating that the size and shape of the scapula are not strongly correlated. Also, the overlap of bipedal basal ornithopods and quadrupedal iguanodontians suggests that the morphological trends are not due solely to locomotion.

Relative warp one accounts for 57.48% of the shape variation in the scapula and explains the variation in shape as the dorso-ventral expansion and anteroposterior shortening of the anterior scapula and the posteroventral expansion of the scapular blade. Negative RW1 scores indicate a narrow scapula without anterior or posteroventral expansion, whereas positive scores indicate a tall anterior scapula with a broadly expanded posteroventral margin. Hadrosaur scapulae are strap-like, maintaining a fairly constant width from scapulocoracoid suture to the posterior margin of the blade. The anterior scapulae of iguanodontians are not strongly dorsoventrally expanded; however, the posterior blade is ventrally expanded. Basal ornithopods trend towards more strongly expanded anterior and posterior margins. The scapulae of *Oryctodromeus* form a distinct group with highly positive RW1 scores indicating a shortened anterior region, which is partially due to medial curvature of the anterior scapula not accounted for in a two-dimensional geometric morphometric analysis, and a strongly expanded posterior margin of the scapular blade.

The second relative warp accounts for 13.50% of the shape variation and describes the rotation of the anterior region relative to the scapular blade: positive values indicate that the scapulocoracoid suture is roughly perpendicular to the scapular blade, whereas negative scores indicate that the scapulocoracoid suture is rotated ventrally relative to the scapular blade. There is no obvious phylogenetic trend visible in RW2: hadrosaurids tend to have negative scores, basal ornithopods, including *Oryctodromeus*, have moderate scores, marginocephalians have positive RW2 scores, and iguanodontians span the entire range of variation.

The CVA (Fig. 7B) indicated that there were four significant canonical variates in explaining the morphology of the scapula (CV1, $p = 5.55 \times 10^{-16}$; CV2, $p = 2.67 \times 10^{-5}$; CV3, $p = 0.0031$; CV4, $p = 0.031$). The first variate is explained by the height of the anterior scapula and by the shape of the posterior blade margin. Positive values indicate a narrower anterior scapula and a less posteroventrally expanded scapular blade. The second variate is explained by the posteroventral expansion of the scapular blade, with positive values indicating a more strongly posteroventrally expanded scapular blade. Variate three is explained by the orientation of the anterior scapula and scapulocoracoid articulation, where a positive value indicates an anteroventrally facing scapulocoracoid articulation and negative values indicate an anteriorly facing scapulocoracoid articulation. Variate four is described by the height of the anterior scapula in opposition to
the shape of the posterior blade margin, where a positive value indicates a taller anterior scapula, and a posterior blade that is not expanded posteroventrally. Unlike the CVA of the humerus, CV1 of the scapula follows a roughly phylogentic trend (Fig. 7B). Specimens of Oryctodromeus remain outliers from basal ornithopods in CV1, due to the tall acromion process of the anterior scapula and the strongly posteroventrally expanded blade. Neither CV2, CV3, nor CV4 has a phylogenetec signal (Fig. 7B, C). Specimens of Oryctodromeus have CV2 scores higher than all other ornithopod groups. Testing the groupings a posteriori, only two specimens were misclassified: one basal ornithopod was misclassified as a basal ornithischian, and one iguanodontian was misclassified as a basal ornithopod.

DISCUSSION

Morphological Trends

Humerus—The PCA, RWA, and CVA of the humerus all indicate that phylogeny and locomotor mode explain the most variation in humeral morphology (Figs. 4, 6A, 7A). However, the morphospace of iguanodontians, basal ornithopods, and hadrosaurids overlap considerably in PC1, PC2, RW1, and RW2 (Figs. 4, 6A). Nevertheless, basal ornithopods typically score at one extreme of the first significant axis of a study (strongly positive in the PC1, strongly negative in both the RW1 and CV1), iguanodontians have intermediate scores, and hadrosaurs score opposite to basal ornithopods (negative in the PCA, and positive in both the RWA and CVA). This shows a morphological trend of more gracile humeri with short, anteriorly projecting deltopectoral crests in basal ornithopods, to more robust humeri with larger, laterally expanded deltopectoral crests in hadrosaurs. The results suggest that most of the shape variation in humeral morphology correlates with the phylogenetic changes in locomotor style, from predominantly bipedal to quadrupedal (Fastovsky and Weishampel, 2005). Positive PC1 scores and negative RW1 scores correlate with the bipedality of basal ornithopods. Only one basal ornithopod, Koreanosaurus, is described as quadrupedal (Huh et al., 2011), and it was not included in this study, so its position in the morphospace is unknown. The overlap in the scores of the ornithopod groups may reflect the gradation of ornithopod phylogeny, because basal ornithopods and iguanodontians are both paraphyletic grades (Butler et al., 2008). Principal component two likely represents a taphonomic influence due to deformed specimens. The strongly gracile humeri and negatively scoring specimens all show a degree of deformation in roughly perpendicular planes that may have generated a morphological signal where none exists naturally. With the exception of specimens of Oryctodromeus, PC3 shows a phylogenetic separation of humeri, with more gracile basal ornithopod humeri with lower scores, and more robust hadrosaurid humeri with positive scores (Fig. 4C). Most specimens of Oryctodromeus exhibit more strongly positive scores in PC1 and PC3 than other basal ornithopods, although there is some overlap of morphospace. Canonical variate one also suggests a strong phylogenetic signal and CV2 shows no separation between ornithopod groups, although CV1 and CV2 scores for specimens of Oryctodromeus show a deviation from both trends (Fig. 7A).

In the first two axes of the PCA and RWA, Oryctodromeus scores within, but at the extreme end of, the ranges present in basal ornithopods, and the third principal component of the PCA indicates that some specimens of the humerus of Oryctodromeus are slightly more robust than those of other basal ornithopods. The CVA shows that Oryctodromeus is distinct from other basal ornithopods in possessing a longer deltopectoral crest and an increased medial offset of the deltopectoral crest relative to other basal ornithopods. A more robust humerus with a more pronounced deltopectoral crest indicates that the humerus may have been specialized for stronger muscle actions relative to other basal ornithopods.

Scapula—Overall, scapular morphology does not correlate with element size, but superficially trends with phylogeny, with Oryctodromeus as an outlier from other basal ornithopods. In all three analyses, variation in scapular morphology is primarily described by the ventral and posterior expansion of the scapular blade, the height of the anterior scapula (associated with the size of the acromion process), and the anteroventral rotation of the scapulocoracoid articulation relative to the orientation of the scapular blade (Figs. 5, 6B, 7B). Hadrosaurids and iguanodontians, with strap-like scapulae with relatively narrow anterior and posterior ends, plot separately from basal ornithopods, which exhibit a more pronounced acromion and ventral expansion of the posterior scapular blade. However, Oryctodromeus does not score similarly to other basal ornithopods, instead exhibiting strongly positive scores reflecting the tall acromion process and strongly expanded posteroventral margin. The traditional morphometric analysis is less consistent with mode of locomotion as an explanatory factor, because Lesothosaurus (NHMUK RU B.17) and specimens of Psittacosaurus, both bipedal, have similar PCI scores to the more quadrupedal hadrosaurids and iguanodontians.

Oryctodromeus has a strongly positive score on the first axes of all three analyses (PC1, RW1, and CV1) and groups separately from other basal ornithopods, indicating strong dorsoventral expansion of the anterior and posterior scapulae. Even relative to other basal ornithopods, the acromion process of Oryctodromeus is extremely narrow and tall. Orodromeus (MOR 623) resembles Oryctodromeus more so than other basal ornithopods because it also bears a tall, narrow acromion with a well-defined scapular spine. The posteroventral expansion of the scapular blade of Oryctodromeus also sets it apart from other ornithopods. Although iguanodontians and basal ornithopods also show a ventral expansion of the scapular blade to varying degrees, in Oryctodromeus the expansion of the scapular blade also extends strongly posteriorly so that the inferior and superior angles of the scapular blade are not the same distance from the scapulocoracoid articulation. The magnitude of the posteroventral expansion is also greater in Oryctodromeus than in other ornithopods.

General Morphological Trends—Overall, the humeral and scapular morphology of ornithopod dinosaurs appears to trend with both phylogeny and locomotor mode. Basal ornithopods exhibit gracile humeri with short, anteriorly projecting deltopectoral crests and do not have CV2 scores within, but at the extreme end of, the ranges present in basal ornithopods. Relative to other basal ornithopods, basal ornithopods have short deltopectoral crests that expand anteriorly, although relative to other basal ornithopods, the humerus of Oryctodromeus is slightly more robust, with an anteromedially projecting deltopectoral crest. The deltopectoral crest acts as an attachment site for many muscle groups used in quadrupedal locomotion and digging, such as the Mm. pectoralis, supracoracoideus, and deltoideus (Dilkes, 2000; Maidment and Barrett.
2011). Thus, deltopectoral crest morphology is important in understanding the functional morphology of the humerus, because a larger deltopectoral crest would allow for greater muscle attachment area, which leads to larger muscles, and stronger muscle actions for the Mm. deltoideus, supracoracoideus, and pectoralis.

Unlike the humerus, the scapula of *Oryctodromeus* is clearly distinct from all other examined taxa in both the traditional and geometric morphometric analyses. Both analyses show that the scapula of *Oryctodromeus* exhibits strong dorsoventral expansion relative to other basal ornithopods. This dorsoventral expansion manifests in two ways: through the broad and posteroventrally expanded scapular blade and through the tall and narrow anterior scapula. Both of these features enlarge the surface area for the insertion of muscle groups that could be beneficial in digging. The dorsoventral expansion of the anterior scapula is primarily due to the increased size of the acromion process relative to other ornithopods. In derived ornithopods, the acromion is relatively short with only a broadly raised region, lacking the well-defined scapular spine present in *Oryctodromeus* and other basal ornithopods.

**Implications for Digging**

As mentioned previously, mammals use three primary types of forelimb digging: hook-and-pull, humeral rotation, and scratch digging. The osteological evidence recognized here for *Oryctodromeus* appears most consistent with scratch digging as the method of constructing burrows. Adaptations for hook-and-pull digging yield large claws and adaptation for strong flexion of the forelimb, such as an expanded medial condyle of the humerus over which flexor muscles pass (Hildebrand, 1985). However, *Oryctodromeus* does not exhibit any expansion of the medial condyle. Unfortunately, the condition of the manual claws is unknown, because those elements have not yet been discovered. However, hook-and-pull digging is used primarily in gathering food rather than in constructing burrows. *Oryctodromeus* also lacks adaptations present in humeral rotation digging, such as a tubercle on the posterior surface of the humeral shaft that acts as an insertion site for the muscles used in digging, and a cranial shift in the glenoid.

The features seen in *Oryctodromeus* are most consistent with adaptations for scratch digging. The scapula of *Oryctodromeus* differs greatly from other basal ornithopods in its dorsoventral expansion. The tall acromion with well-defined scapular spine allows a greater surface area for muscle attachment for groups such as the M. deltoideus clavicularis and M. supracoracoideus (Maidment and Barrett, 2011). The broadly expanded scapular blade would have increased the surface area of the broad origin of the M. deltoideus scapularis (Maidment and Barrett, 2011), a muscle important in digging in mammals (Hildebrand, 1985). The humerus lacks an expanded medial condyle as seen in scratch-digging mammals. However, the slightly more robust quality of the humerus relative to other basal ornithopods indicates adaptation for increased forces from the muscles originating and inserting on the humerus. The shape of the coracoid remains morphologically conservative throughout ornithopod phylogeny, and our analyses were unable to recognize any specializations potentially related to digging or any other purpose (see Supplementary Data). One caveat to this interpretation is that our analyses did not incorporate a measure of element size relative to the entire body or other elements. Thus, we did not quantify what would appear to be an unusually large coracoid relative to other ornithopods, with a dorsoventral height that is 52.4% of humeral length in *Oryctodromeus* (Varricchio et al., 2007:fig. 4). Nevertheless, the features on the other elements examined indicate that the forelimb and pectoral girdle of *Oryctodromeus* do exhibit osteological specializations beneficial for digging relative to other ornithopod dinosaurs.

**Limitations of this Study**

Although the evidence supports the presence of morphological specializations beneficial for digging in *Oryctodromeus*, it is important to note that the comparison of *Oryctodromeus* with mammals is a level III inference (Witmer, 1985). Level III inferences imply a high degree of uncertainty when reconstructing soft tissue adaptations for behaviors. However, this high degree of uncertainty is inevitable, because the extant phylogenetic bracket of *Oryctodromeus* does not contain examples of archosaurs with adaptations for digging and so is of little help in this morphometric analysis. The forelimb morphology of mammals and archosaurs, although grossly homologous, proves difficult to compare directly with one another, because it is difficult to locate homologous structures on each element, especially in fossil taxa. Therefore, only broad generalizations about morphological specialization for digging in dinosaurs can be made. Despite the uncertainty of a level III inference, when the abundance of modern organisms that construct burrows without morphological specialization for digging (i.e., prairie dogs, rabbits, and digging carnivores such as foxes and dogs; Hildebrand, 1985) is considered, the presence of any morphological specialization beneficial to digging supports the hypothesis.

Another potential limitation of this study is the loss of morphological information due to the methods of morphometric analyses. A three-dimensional geometric morphometric analysis to describe shape variation would be most informative, especially for the humerus, because it utilizes the third dimension more fully than the relatively flat scapula. However, the lack of necessary equipment necessitated the use of two-dimensional geometric morphometrics. The use of traditional morphometrics is limited by the fact that overall shape data can be lost when just taking a series of measurements, because there is no way to know the relative position of one measurement to another. However, the limitations of each of these methods did not appear to influence the study too strongly, because both methods produced very similar results. Therefore, the two morphometric methods could be used to test the validity of the other, and it appears that the consistency of the two methods indicates that most of the morphological information was captured in the study. The morphometric analysis is also hindered by the small sample sizes, within individual taxa and overall, which is especially evident in the results of the analysis of the coracoid (see Supplementary Data).

**CONCLUSION**

The morphometric analyses showed that ornithopod morphology trends with mode of locomotion. Larger quadrupedal ornithopods have a more strap-like scapula and a humerus with a long, laterally offset deltopectoral crest, and smaller bipedal ornithopods have humeri with shorter, anteriorly oriented deltopectoral crests and scapulae with more pronounced acromion processes and an expanded posterior scapular blade.

Although the potential for digging in dinosaurs has only recently been suggested, the most compelling evidence for digging is *Oryctodromeus*, which is supported by both taphonomic evidence (Varricchio et al., 2007; Woodruff and Varricchio, 2011) and the morphological evidence presented herein and in its original description (Varricchio et al., 2007). Although coracoid shape does not appear to be specialized for digging, the humerus of *Oryctodromeus* is slightly more robust relative to humeral length than other basal ornithopods. When the morphology of phylogenetic groups is examined, the humerus of *Oryctodromeus* does not group with those of other basal ornithopods. The scapula of *Oryctodromeus* is more specialized, with a
strongly expanded posteroventral margin of the examined scapular blade and tall acromion process. A more robust humerus, expanded posteroventral margin of the scapula, and long acromion process are all advantageous adaptations for digging and correspond with the adaptations for digging seen in mammals. Although not analyzed in this study, the ulnae of *Oryctodromeus* do not appear specialized for digging, because the olecranon process is short.

The limb proportions of *Oryctodromeus* indicate that it was fully bipedal (Varricchio et al., 2007), not facultatively bipedal or quadrupedal. Therefore, the more robust quality of the humerus is not associated with a change in locomotor style, nor are the specializations observed in the scapula consistent with facultative bipedalism or quadrupedalism. Phylogenetic analyses of ornithopods consistently place *Oryctodromeus* as a basal member of the ornithopod lineage, not closely related to the more robust iguanodontians. Neither locomotion nor phylogeny provides an adequate alternative hypothesis for the morphological features seen in the forelimb of *Oryctodromeus*. The forelimb adaptations, lack of hind limb modifications for non-cursorial lifestyles such as swimming or climbing (Varricchio et al., 2007), and its discovery in a burrow lead to digging as the most parsimonious hypothesis.

Despite the limitations of this study, useful morphological information can be gained by morphometric analyses. Both the traditional and geometric morphometric analyses provided consistent summaries of the morphospace of ornithopod forelimbs, indicating that there was no severe loss of morphological data. Although the lack of analogues for digging in the EPB makes inferences more difficult, generalizations can be made with some confidence. Although there was little information about mammals exhibiting moderate or adaptation of only the scapula for digging, the existence of burrowing organisms with no adaptations for digging (Hildebrand, 1985) indicates the possibility of burrowing without extreme osteological adaptation. The relative robustness of the humerus of *Oryctodromeus* and the expanded acromion process and posterior blade margin of the scapula both point to adaptations for scratch digging.

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APPENDIX 1. Specimens and group assignments used for the traditional and geometric morphometric analyses (H, humerus; S, scapula). An ‘x’ indicates the inclusion of one specimen in an analysis; numerals indicate the inclusion of multiple elements associated with one specimen number.

| Specimen   | Taxon                     | Group                | Traditional | Geometric |
|------------|--------------------------|----------------------|-------------|-----------|
|            |                          |                      | H           | S         |
| BYU 631-163| *Othnielosaurus consors* | Basal Ornithischia   | x           | x         |
| BYU 16719  | *Othnielosaurus* sp.     | Basal Ornithischia   | x           |           |
| NHMUK R11000 | *Stormbergia damageshoeki* | Basal Ornithischia | x           |           |
| NHMUK R B.17 | *Lesothosaurus diagnosticus* | Basal Ornithischia | x           | x         |
| MOR 1642   | *Oryctodromeus cubicularis* | Basal Ornithopoda    | 3           | 2         |
| MOR 1636a  | *Oryctodromeus cubicularis* | Basal Ornithopoda    | x           | 2         |
| IMNH 44951 | *Oryctodromeus cubicularis* | Basal Ornithopoda    | x           |           |
| MOR 404    | *Orodromeus makelai*     | Basal Ornithopoda    | x           | x         |
| MOR 294    | *Orodromeus makelai*     | Basal Ornithopoda    | x           | x         |
| MOR 473    | *Orodromeus makelai*     | Basal Ornithopoda    | x           |           |
| MOR HC-164 | *Thescelosaurus* sp.     | Basal Ornithopoda    | x           |           |
| CM 9900    | *Thescelosaurus* neglectus | Basal Ornithopoda    | x           |           |
| NHMUK R192 | *Hypsilophodon foxi*     | Basal Ornithopoda    | x           |           |
| NHMUK R194 | *Hypsilophodon foxi*     | Basal Ornithopoda    | x           |           |
| NHMUK R196 | *Hypsilophodon foxi*     | Basal Ornithopoda    | 2           | 2         |
| NHMUK R3830 | *Hypsilophodon foxi*   | Basal Ornithopoda    | x           |           |
| FMNH IGM 100/2015 | *Haya griggii*   | Basal Ornithopoda    | x           | x         |
| UMNH VP20644 | *Unnamed hypsilophodontid* | Basal Ornithopoda    | x           |           |
| MOR 548    | Lambeosaur indet.        | Hadrosauridae        | 7           | 3         |
| MOR 547    | *Maiasaura peeblesorum* | Hadrosauridae        | 2           | 2         |
| YPM-PU 22400 | *Maiasaura peeblesorum* | Hadrosauridae        | 2           |           |
| YPM-PU 23444 | *Maiasaura*             | Hadrosauridae        | x           |           |
| MOR 478    | *Gryposaurus latidens*   | Hadrosauridae        | x           |           |
| MOR 1071   | *Brachylophosaurus canadensis* | Hadrosauridae | 4           | 2         |
| MOR 311    | Hadrosaurine indet.      | Hadrosauridae        | x           |           |
| YPM-PU 23255 | *Hadrosaurus*           | Hadrosauridae        |              |           |
| MOR 607    | Hadrosaur indet.         | Hadrosauridae        | x           | x         |
| YPM 3454   | Hadrosaur indet.         | Hadrosauridae        | x           |           |
| BYU 12192  | Hadrosaur indet.         | Hadrosauridae        | x           |           |
| CM 1066    | Hadrosaur indet.         | Hadrosauridae        | x           |           |
| CM 3025    | *Edmontosaurus* sp.      | Hadrosauridae        | x           |           |
| NHMUK R3640 | *‘Trachodon’* sp.      | Hadrosauridae        | x           |           |
| CM 9461    | *Corythosaurus casaurus* | Hadrosauridae        | x           | x         |
| DBDP-42    | *Unnamed iguanodontian* | Iguanodontia         | x           |           |
| DBJP-119   | *Unnamed iguanodontian* | Iguanodontia         | x           |           |
| YPM-PU 23255 | *Unnamed iguanodontian* | Iguanodontia         | x           |           |
| DBDP-185   | *Unnamed iguanodontian* | Iguanodontia         | x           |           |
| UMNH VP20208 | *Hippodraco scutodens* | Iguanodontia         | x           |           |
| BYU 17948  | *Camptosaurus* sp.       | Iguanodontia         | x           |           |
| BYU 17945  | *Camptosaurus* sp.       | Iguanodontia         | x           |           |
| UMNH VP16567 | *Camptosaurus*        | Iguanodontia         | x           |           |
| CM 11337   | *Camptosaurus aphanoeetes* | Iguanodontia       | 2           | 2         |
| YPM 1877   | *Camptosaurus dispar*    | Iguanodontia         | x           | x         |
| YPM 1878   | *Camptosaurus dispar*    | Iguanodontia         | x           |           |
| YPM 1800   | *Camptosaurus dispar*    | Iguanodontia         | 2           | 2         |
| YPM 56454  | *Camptosaurus dispar*    | Iguanodontia         | x           |           |
| YPM 6794   | *Camptosaurus medius*    | Iguanodontia         | x           |           |
| YPM 7331   | *Camptosaurus medius*    | Iguanodontia         | x           |           |
| YPM 8611   | *Camptosaurus medius*    | Iguanodontia         | x           |           |
| YPM 5456   | *Tenontosaurus tilletti* | Iguanodontia         | 2           | 2         |
| YPM-PU 16514 | *Tenontosaurus tilletti* | Iguanodontia       | x           |           |
| FMNH PR2263 | *Tenontosaurus tilletti* | Iguanodontia         | x           |           |
| MOR 682    | *Tenontosaurus tilletti* | Iguanodontia         | x           |           |
| MOR 2558   | *Tenontosaurus tilletti* | Iguanodontia         | x           |           |
| CM 3392    | *Dryosaurus alutus*      | Iguanodontia         | x           |           |
| CM3392/21786 | *Dryosaurus alutus*   | Iguanodontia         | 2           | 2         |
| YPM 1876   | *Dryosaurus alutus*      | Iguanodontia         | x           |           |
| BYU 5215   | *Dryosaurus* sp.         | Iguanodontia         | x           |           |
| CM 21786   | *Dryosaurus* sp.         | Iguanodontia         | x           |           |
| NHMUK R2519 | *Iguanodon* sp.         | Iguanodontia         | x           |           |
| NHM UK R116 | *‘Iguanodon mantelli’*   | Iguanodontia         | x           |           |
| NHMUK R2196 | *‘Iguanodon mantelli’*   | Iguanodontia         | x           |           |
| NHMUK R966 | *Barilium dawsoni*      | Marginocephalia      | x           |           |
| NHMUK R4743 | *Barilium dawsoni*     | Marginocephalia      | x           |           |
| CM 9185    | *Protoceratops andrewsi* | Marginocephalia      | x           | x         |
| FMNH IGM 100/1930 | *Psittacosaurus mongoliensis* | Marginocephalia | x           |           |
| U of C LHPV2 | *Psittacosaurus gobiensis* | Marginocephalia     | 2           | 2         |

Fearon and Varricchio—Forelimb morphometrics of *Oryctodromeus* (e936555-14)