SCRATCH-DIGGING IN THE CRETACEOUS BASAL ORNITHOPOD DINOSAUR *ORYCTODROMEUS CUBICULARIS*: EVIDENCE FROM MORPHOMETRIC ANALYSES AND RECONSTRUCTION OF THE FORELIMB MUSCULATURE

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ABSTRACT

The basal ornithopod dinosaur *Oryctodromeus cubicularis* was discovered within a burrow structure in the mid-Cretaceous Blackleaf Formation of western Montana. This, and features of the pelvis, skull, and forelimbs also seen in burrowing mammals led to the interpretation of *Oryctodromeus* as the first formally described burrowing dinosaur. This study further describes the forelimb specialization of *Oryctodromeus* and analyzes the validity of the interpretation of *Oryctodromeus* as adapted for digging using morphometric analyses and muscular reconstructions of the humerus, scapula, and coracoid. The morphometric analyses used two methods, including traditional morphometrics using principal component analysis of a series of element length measurements and geometric morphometrics using relative warp analysis of a series of landmarks superimposed on photographs of elements. Both methods reduce the number of variables to explain the greatest amount of variation between specimens. Results indicated that the humerus of *Oryctodromeus* is slightly more robust than other basal ornithopods, the coracoid exhibits no specialization for digging, and the scapula is strongly specialized, with a long narrow acromion and strongly expanded posteroventral margin of the scapular blade providing greater surface area for muscle attachment. Reconstruction of the forelimb musculature was generated by comparing both the presence or absence of muscles and the locations of attachment sites between birds and crocodilians, the extant phylogenetic bracket of dinosaur, and by examination of specimens of *Oryctodromeus* and other ornithopods for osteological correlates. Muscle groups used for burrowing in mammals include the deltoideus scapularis, latissimus dorsi, triceps longus, and teres major. The first three are present in *Oryctodromeus*, but the presence of the teres major is equivocal. The strongly expanded posteroventral scapula indicates an increased surface area for the origin of the deltoideus scapularis and possibly teres major. This expanded area would be advantageous for burrowing. The origin of the triceps longus near the glenoid of the scapula would not provide strong extension of the antebrachium, a motion important in scratch-digging. The osteology and musculature both provide evidence of slight adaptation for scratch-digging in *Oryctodromeus.* As many vertebrates burrow without morphological specializations, the presence of these features sufficiently supports adaptation for burrowing in *Oryctodromeus.*

INTRODUCTION

Focus of Study

Non-avian dinosaurs inhabited a surprisingly limited niche space, considering the longevity and diversity of the group. Dinosaurs remained primarily terrestrial, and are rarely considered to inhabit aquatic, arboreal, or fossorial niches. The description of *Oryctodromeus* as burrowing marks the expansion of dinosaur niche space occupation into a habitat previously thought to be inhabited primarily by mammals. *Oryctodromeus cubicularis* is a hypsilophodontid grade ornithopod that was discovered within a burrow structure. The association of an adult and two juvenile specimens within a burrow trace, as well as morphological features which were described as potentially advantageous for digging, prompted Varricchio et al. (2007) to suggest that *Oryctodromeus* was a denning dinosaur, constructing burrows to rear young.

Previous to the description of *Oryctodromeus*, Bakker (1996) mentioned the basal ornithopod *Drinker* as living in communal burrows, but did not fully describe the specimens or burrow structure. But since the description of *Oryctodromeus*, the exploration of fossorial niche space use by dinosaurs has significantly expanded. Many other cases of digging and denning have since been described within dinosaurs. Martin (2009) described burrow structures similar to the one associated with *Oryctodromeus* from the Otway Group in Australia, and suggested a Gondwanan hypsilophodontid as the burrow maker. Hypsilophodontid *Koreanosaurus* from South Korea was also described as potentially burrowing (Huh et al., 2010). Longrich (2010) hypothesized that

Protoceratops constructed dens in sandy substrate and Senter (2007) suggested *Leptoceratops* and *Protoceratops* exhibited osteological features beneficial for digging such as a short manus. Fowler & Hall (2010) proposed sauropods used their pes to dig nests in a motion somewhat like that used by turtles. Digging in theropods has been described as a means of obtaining food for Alvarezsaurids such as Mononykus (Senter, 2005), and Abelisaurids (Sereno, 2010). Simpson et al. (2010) described theropod claw traces in burrow structures indicating attempted digging in pursuit of prey.

To support the hypothesis that *Oryctodromeus* constructed burrows, Varricchio et al. (2007) described potential morphological adaptations for digging present in the adult specimen of *Oryctodromeus*, including fused premaxillae, an expanded sacrum and greater attachment area between the pelvis and sacrum relative to other basal ornithopods for stability while digging, and a robust, fused scapulocoracoid with a prominent scapular spine. However, very little manus material and no manual unguals have been uncovered for *Oryctodromeus*. Additionally, an adult specimen found without any burrow traces exhibits a series of ossified tendons above the tail and hips, which might have limited the mobility of adults within a burrow. Therefore, the raw morphological data with regards to whether *Oryctodromeus* constructed the burrow with which it was associated is inconclusive, and needs further examination.

Purpose of Study

Little work has been done on shoulder and forelimb morphometrics of ornithopod dinosaurs, whether to understand digging in ornithopods or for other research goals such

as locomotion. Nor is there much quantitative information about the morphological specialization for digging in dinosaurs, crocodilians, other reptiles, or bipedal animals. Traditional and geometric morphometric analyses are methods by which the forelimb morphology of *Oryctodromeus* can be quantitatively described and compared with other ornithopod dinosaurs. If the morphology of *Oryctodromeus*, and potentially other closely related ornithopods, shows specialization consistent with the adaptations for digging seen in other vertebrates, then it supports the hypothesis that *Oryctodromeus* was adapted for constructing burrows, rather than utilizing stolen burrows. Chapter 3 of this thesis explores the morphometric analysis of the scapula, coracoid, and humerus of ornithischian dinosaurs in an effort to quantitatively compare ornithopod morphology and the significance of the morphological adaptations within *Oryctodromeus.*

Though the osteology of dinosaur and mammal pectoral girdles and forelimbs are homologous, their morphology is vastly different. In dinosaurs the scapula and coracoid are both prominent, the sternal plate is simple, and the clavicle (known as the furcula in dinosaurs when the left and right clavicles are fused) is only present in some taxa, whereas in mammals, the scapula is prominent, the coracoid has been reduced to a small process of the scapula, the clavicle can vary in prominence within mammals, and the sternum is more complex and more strongly associated with the ribs (Kent and Carr, 2008). The humeri also differ in that dinosaur humeri have a deltopectoral crest projecting anteriorly, and the proximal and distal ends are comparatively simple, likely due to the presence of cartilaginous epiphyses that are not preserved (Holliday et al., 2010), whereas mammals lack a deltopectoral crest and have complex articular surfaces

(Kent and Carr, 2008). Due to these differences, specific osteological correlates for digging behavior cannot be compared directly between mammals and dinosaurs; however the overall function and interactions between the skeleton and musculature are very similar. Therefore, broad generalizations in adaptations for digging and adaptations involving similar muscle groups provide a basis of comparison. Therefore, Chapter 4 outlines the muscle reconstruction generated to understand the functional significance of osteological specializations in *Oryctodromeus*.

LITERATURE REVIEW

Digging is a behavior that has only recently been explored in dinosaurs (Bakker, 1996; Longrich, 2010; Senter, 2005; Senter, 2007; Varricchio et al., 2007; Martin, 2009; Simpson et al., 2010; Fowler and Hall, 2010; Huh et al., 2010). One of the most interesting discoveries regarding digging in dinosaurs was the basal ornithopod *Oryctodromeus cubicularis*, which was described as potentially constructing burrows by digging with its forelimbs (Varricchio et al., 2007). *Oryctodromeus* was first discovered in the early Upper Cretaceous Blackleaf Formation of Montana (Varricchio et al., 2007); additional specimens of *Oryctodromeus* have been described from the Wayan Formation in Idaho, a formation equivalent to the Blackleaf (Krumenacker, 2010). It is a basal ornithopod, most closely related to *Orodromeus* and *Zephyrosaurus*, other Montanan ornithopods (Varricchio et al., 2007). The holotype (MOR 1636a) and paratype (MOR 1636b) material were found in a preserved burrow structure greater than 2 m long. The burrow structure cuts a mudstone layer, and is infilled with stratified sandstone, and the three skeletons were disarticulated within the burrow chamber (Varricchio et al., 2007). An actualistic study attempted to produce these disarticulation and sedimentary patterns observed using a model of the burrow structure and rabbit bones (Woodruff and Varricchio, 2011). Their experiment determined that the disarticulation pattern discovered is possible for skeletons already in the burrow, rather than having been transported in already disarticulated. Both actualistic and sedimentological taphonomic evidence supports the hypothesis that *Oryctodromeus* was associated in life with the burrow in which it was discovered. Varricchio et al. (2007) also describes potential

morphological features beneficial for digging present in the adult specimen of *Oryctodromeus*, including expanded and fused premaxillae, pelvic features such as an expanded sacrum and greater attachment area between the pelvis and sacrum relative to other basal ornithopods, and a robust, fused scapulocoracoid with a prominent scapular spine. However, very little manus material and no manual unguals, which commonly exhibit specializations for digging in many taxa (Hildebrand, 1985), were discovered during excavation. Additionally, the presence of ossified tendons above the tail and hips in a larger adult specimen (MOR 1642) might have limited the mobility of adults within a burrow.

Because the morphologic data is somewhat inconclusive as to whether *Oryctodromeus* constructed the burrow with which it was associated, further examination of the morphology is necessary. Using traditional and geometric morphometric analyses to quantitatively describe and compare *Oryctodromeus* with other ornithopod dinosaurs can determine whether the forelimbs of *Oryctodromeus* are outliers of any morphologic trends within Ornithopoda, or if *Oryctodromeus* clustered with *Orodromeus*, the sister taxon to *Oryctodromeus*, indicating that they may have also created burrows, as suggested by Varricchio et al. (2007), or whether *Oryctodromeus* does not exhibit significant morphological specialization when compared to other ornithopods. If the results indicated that *Oryctodromeus* did not exhibit forelimb morphology significantly different than other ornithopods, it would indicate that *Oryctodromeus* was not morphologically specialized for digging. In this case, the specimens of *Oryctodromeus* found within the burrow structure may have stolen the burrow from another animal, or

Oryctodromeus may have been able to construct a burrow but lacked specialized forelimb morphology for the behavior, as is seen in some mammals. Additionally, musculature reconstruction can be used to determine the impacts of any osteological morphological specialization seen in the forelimb on the soft-tissue anatomy of *Oryctodromeus,* as specialized features might correspond with the musculature used for digging.

Morphology of Digging

Burrowing behavior is fairly common in mammals and reptiles, and uncommon in birds. There have been several behavioral studies associated with burrowing in mammals and other vertebrates, however fewer biomechanical and morphometric studies have been conducted. Compared to other vertebrate groups, the morphological adaptations for digging in mammals have been well explored. Some mammals exhibit extreme morphological adaptations for a completely fossorial lifestyle, however many do not exhibit any morphological adaptations despite exhibiting digging behaviors. Hildebrand (1985) summarized the various morphological adaptations for digging and burrowing in quadrupedal vertebrates, primarily mammals. Depending on the digging style, morphological adaptations for digging can include strong incisors and tougher snouts with stronger rostra, stronger forelimb muscles, an enlarged medial epicondyle of the humerus, enlarged olecranon process, large claws which are either sharp and laterally compressed for loosening soil or broad and blunt for moving soil, and fusion of sacral and pelvic elements for bracing while digging.

A study of cingulate (armadillo and glyptodont) humeri determined that in smaller cingulates with more fossorial behavior, the humerus became more robust with more powerful muscle attachment sites and a stronger elbow joint, but with larger cingulates such as glyptodonts, humeral shape was more strongly related to size than to function (Milne et al., 2009). Another study determined that fossoriality was related to the ratio of length of the olecranon process to the total ulnar length, or the Index of Fossorial Ability (IFA), in cingulates (Vizcaino et al., 1999). In caviomorphs (chinchillas, capybaras, etc.) the IFA and the robustness of the humerus and ulna increase with increasing fossoriality (Elissamburu and Vizcaíno, 2004).

Most burrowing mammals are quadrupedal, whereas *Oryctodromeus* was a bipedal ornithopod dinosaur. Thus the forelimb morphology of *Oryctodromeus* was influenced by different functional and evolutionary pressures than those of quadrupedal mammals, and therefore may exhibit different morphological specializations. Bipedalism might allow the forelimb to become specialized for a particular behavior as it no longer serves a major role in locomotion, but it also allows the forelimb to become available for multiple uses which that act to maintain a generalized morphology. A study on the forelimbs of burrowing heteromyids (kangaroo rats and kangaroo mice) indicated only a slight morphological difference in forelimb shapes and proportions between bipedal and quadrupedal burrowers (Price, 1993).

Fossorial behavior in extant archosaurs has been described in both birds and crocodilians, ranging in magnitude from digging on the surface of the ground to burrowing. Though birds, like basal ornithopods, are bipedal, most digging and

burrowing is done with the hind limbs rather than the forelimbs or beaks, such as in the burrowing owl and Magellanic penguin (Stokes and Boersma, 1991). Therefore, birds are an inadequate analog for forelimb morphology and burrowing adaptations. Among reptiles, there have been some behavioral studies, but relatively few morphological studies of digging. In the gopher tortoise, morphological adaptations include broadening of the unguals and shortening of the manus, and more robust forelimb bones (Bramble, 1982). However, burrowing lepidosaurs often exhibit very little morphological differentiation between burrowing and non-burrowing varieties (Kley and Kearney, 2007). Studies of digging crocodiles indicate that they can dig with their forelimbs in a lateral sweeping motion, but the morphological features of the forelimb are more strongly related to their semiaquatic lifestyle, rather than their digging behavior (Kley and Kearney, 2007). Because of the difference in gait and lifestyle, crocodilians do not serve as an adequate analog for ornithopod forelimbs either.

Forelimb Musculature

When looking at functional morphology, bone-muscle interaction is an important factor to understanding the lifestyle and locomotion of an organism. In mammals, the muscle groups primarily used in burrowing are the teres major, the deltoideus, the scapular head of the triceps, the dorsoepitrochlearis, and latissimus dorsi (Hildebrand, 1985). These muscles generally attach distal to the glenoid on the scapula and relatively distally on the humerus, on the olecranon process of the ulna, or on the proximal radius. This provides a more powerful lever arm in digging.

Using direct evidence of the position and extent of muscle attachment sites from fossil bone would be an ideal method of reconstructing musculature. The presence of osteological correlates, features on the bone which indicate the presence of a muscular or tendinous attachment, can be helpful in describing the presence and position of muscle groups. However osteological correlates do not indicate the full extent of a muscle attachment site, and absence of osteological correlates do not necessarily indicate absence of a muscle group. Studies of both mammals and birds warn against the use of osteological correlates as a basis for muscle reconstruction (McGowan, 1986, Bryant and Seymour, 2005). Tendinous and aponeurotic attachment sites were most likely to generate osteological correlates than fleshy, direct muscle attachment sites, though neither type was likely to preserve the entire extent of the attachment in carnivorans (Bryant and Seymour, 2005), and osteological correlates are more commonly found in mammals than in birds and reptiles (Bryant and Seymour, 2005). In the weka (*Gallirallus australis*), a flightless carinate, only about 30% of the forelimb muscles corresponded with osteological correlates (McGowan, 1986), whereas in *Canis* and *Ursus*, about 80% of muscles corresponded with osteological correlates (Bryant and Seymour, 2005).

Instead of relying solely on osteological correlates, the extant phylogenetic bracket (EPB) of dinosaurs can help elucidate hypotheses regarding soft tissue. By analyzing the soft tissue anatomy of birds and crocodilians, which are the closest extant taxa to dinosaurs, one can determine whether the presence of a soft tissue feature is strongly, weakly, or not supported by the EPB. Bryant and Russell (1992) and Witmer

(1995) introduced similar methods for examining the EPB in order to infer soft tissue anatomy in extinct taxa, including generating hierarchies of the certainty of inferences.

For example, one of the primary muscle groups used in digging in mammals is the teres major. However the teres major is equivocally present within dinosaurs. The EPB does not fully support the presence of a teres major within dinosaurs, as it is not present in birds (Howell, 1937), but it is present in crocodilians (Reese, 1915). Because of this uncertainty, muscular analyses of *Maiasaura* (Dilkes, 2000) and *Lesothosaurus* (Maidment and Barrett, 2011) exclude the teres major from reconstructions; although in the muscle reconstruction of *Camptosaurus*, Carpenter and Wilson (2008) included the teres major.

Digging in Dinosaurs

Digging is a behavior that has only recently been explored in dinosaurs, and in most cases it is limited to scratch-digging on the surface. Within theropods, Senter (2005) proposed that the alvarezsaur *Mononykus* used its reduced forelimbs for scratch-digging into insect mounds, and Longrich and Currie (2009) suggested the forelimbs of the closely related *Albertonykus* were specialized for digging, not in the soil, but into termites nesting in wood. Sereno (2010) described a Noasaurid theropod as fossorial due to its straight unguals, small yet robust forelimb, and enlarged coracoid, proposing they enlarged the burrows of prey during pursuit. Similarly, maniraptoran theropod claw marks within small mammal burrow structures indicate the presence of predatory digging behavior within dinosaurs (Simpson et al., 2010). Fowler and Hall (2010) described the

pedal unguals of sauropods as adapted for scratch-digging and used in nest building like turtles. Scratch-digging in basal ceratopsians such as *Leptoceratops* and *Protoceratops* has been suggested by Senter (2007).

However, the potential for burrowing has been described only in the basal ornithopods *Drinker* (Bakker, 1996), *Koreanosaurus* (Huh et al., 2010), and *Oryctodromeus* (Varricchio et al., 2007). Bakker (1996) mentions the presence of several specimens of *Drinker* living within a communal burrow in a swampy environment; however he does not fully describe the sedimentology or any potential morphological adaptations. Huh et al. (2010) described *Koreanosaurus* as potentially burrowing due to its morphological similarities to *Oryctodromeus*, as well as taphonomic evidence such as 3D preservation within a paleosol and lack of evidence of carnivory. Additionally, burrow structures of similar size and shape to the one in which *Oryctodromeus* was discovered were described from the Otway Group in Australia, and though there were no body fossils within the structures, the fauna of the Otway group does include ornithopods (Martin, 2009).

Phylogenetic Framework

Oryctodromeus is traditionally considered a hypsilophodontid grade ornithopod, however the phylogeny of hypsilophodontids is highly debated. Butler et al. (2008) found that both Ornithopoda and Hypsilophidontidae are polyphyletic grades containing both basal neornithischians as well as basal ornithopods. Several phylogenetic trees have been proposed using different analytical methods, producing sometimes highly variable

results and extensive polytomies. Boyd et al. (2009) found a strict consensus tree that produced a monophyletic clade including *Oryctodromeus, Orodromeus, Zephyrosaurus,* and *Thescelosaurus*, to the exclusion of *Hypsilophodon*. *Lesothosaurus* places as the basalmost Thyreophoran, and *Stormbergia* consistently ranks as basal Ornithischian, and *Othnielosaurus,* which was initially described as a basal ornithopod (Galton and Jensen, 1973), is now more often classified as a basal neornithischian (Butler et al., 2008). Using the data matrix of Scheetz (1999), Varricchio et al. (2007) found that *Oryctodromeus* is most closely related to *Orodromeus makelai* of the Two Medicine Formation in Montana (Horner and Weishampel, 1988; Scheetz, 1999) and *Zephyrosaurus schaffi* of the Cloverly Formation in Montana (Sues, 1980). Due to the morphological similarity between these three genera Varricchio et al. (2007) suggested that *Orodromeus* and *Zephyrosaurus* may have also constructed burrows. *Koreanosaurus* also belongs to the *Orodromeus-Zephyrosaurus-Oryctodromeus* clade and is hypothesized to have constructed burrows (Huh et al., 2010). *Thescelosaurus* consistently ranked as a basal ornithopod more derived than *Oryctodromeus* (Butler et al., 2008). A more recent but preliminary study indicates that the clade consisting of *Oryctodromeus*, *Orodromeus, Zephyrosaurus, Koreanosaurus,* and *Thescelosaurus* are not basal ornithopods, but basal neornithischians positioned outside of Cerapoda (Boyd, 2012).

The analysis presented here also includes more derived ornithopods such as the basal iguanodontians *Tenontosaurus* and *Dryosaurus,* and Ankylopollexians (or the common ancestor of *Camptosaurus* and *Parasaurolophus* all its descendants) such as *Camptosaurus* and *Tenontosaurus*, other iguanodontians, and hadrosaurs such as

Maiasaura and *Brachylophosaurus.* This allows the morphometric analysis to show any morphological changes due to the trend of increasing quadrupedality in ornithopods. Outgroups in this analysis include basal neornithischians *Othnielosaurus* and *Stormbergia* and basal thyreophoran *Lesothosaurus* (Butler et al., 2008), which will be hereafter referred to collectively as basal ornithischians, as well as marginocephalians *Protoceratops* and *Psittacosaurus*. The basal ornithischians included in this analysis have historically unstable phylogenetic positions, with some being classified as basal ornithopods, basal neornithischians (which exclude heterodontosaurs and thyreophorans), or basal ornithischians in the past (Norman et al., 2004a; Norman et al., 2004b).

Morphometrics

Oryctodromeus cubicularis has been described as burrowing due to the discovery of an adult and two juvenile specimens within a burrow structure, as well as the presence of morphological adaptations potentially advantageous for digging with its forelimbs (Varricchio et al., 2007). In order to quantitatively describe the forelimb morphology of *Oryctodromeus* and how it differs from other ornithopod dinosaurs, traditional and geometric morphometric analyses were run on forelimb and pectoral girdle elements. Though several morphometric analyses have been performed on cranial elements, morphometric analysis of postcranial elements is less refined; where cranial elements have several points which can be easily recognized across taxa, postcranial elements are more difficult to analyze due to the lack of easily correlated homologous landmarks. Studies on postcranial morphometrics have been conducted to determine phylogenetic

relationships, species identification, potential dimorphism, and locomotor biomechanics of various dinosaur groups. In a study of hadrosaur taxonomy using pelvic morphology, it was determined that the use of inflection points as a means of comparing different specimens yielded good results for species identification, but was less useful in determining phylogeny (Chapman and Brett-Surman, 1990). A study of *Plateosaurus* femora used muscle attachment sites and gross morphology of the bone as a means with which to compare different specimens to determine if there were multiple distinct morphologies within a species (Weishampel and Chapman, 1990). However, fewer studies have been conducted attempting to morphometrically describe functional adaptations. Pedal phalanx morphology of several theropod dinosaurs was measured and compared with the phalanx morphology of modern birds in order to determine if there was any correlation with lifestyle (Kambic, 2008). Using traditional morphometrics (a series of measurements of lengths and widths), and geometric morphometrics (analyzing shape using homologous landmarks), the scapular, coracoid, and humeral morphology of several ornithischian dinosaurs were analyzed to determine where *Oryctodromeus* is categorized in the morphospace of ornithopod forelimbs.

CHAPTER THREE

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

Contribution of Authors and Co-Authors

Manuscripts in Chapters 3 and 4

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Contributions: Obtained grants, collected and analyzed data, wrote manuscript.

Co-Author: David J. Varricchio

Contributions: Collected a majority of *Oryctodromeus* specimens, provided significant edits to grant proposals and manuscripts.

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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 several morphological features considered consistent with burrowing. Using traditional and geometric morphometric analyses, the morphology of the humerus, scapula, and coracoid of ornithopods, basal ornithischians, and marginocephalians, was analyzed to describe and characterize quantitatively the differences in forelimb morphology between *Oryctodromeus* and other ornithopods. These differences were then compared to the morphological adaptations for digging in mammals, as there are no adequate analogs for burrowing in extant archosaurs. A canonical variates analysis was also conducted on the geometric morphometric data to determine if phylogeny impacted morphological trends. Morphometric results indicate that the coracoid exhibits no adaptations beneficial to digging, and appears to be morphologically conservative throughout ornithopod phylogeny. 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 posteroventrally expanded scapular blade provide surface areas for the attachment of the supracoracoideus, deltoideus clavicularis, and

deltoideus scapularis muscles, the latter which is important in digging in mammals. These features provide evidence for specialization for producing burrows by scratch-digging.

INTRODUCTION

Digging is a behavior that has only recently been explored in dinosaurs (Bakker, 1996; Senter, 2005; Senter, 2007; Varricchio et al., 2007; Martin, 2009; Sereno, 2010; Simpson et al., 2010; Fowler and Hall, 2010; Huh et al., 2010). One of the most interesting discoveries regarding digging in dinosaurs was the basal ornithopod *Oryctodromeus cubicularis*, which was described as potentially constructing burrows with its forelimbs (Varricchio et al., 2007) due to its discovery in a burrow structure, and morphological features potentially advantageous for digging, such as expanded and fused premaxillae, expanded sacrum and greater attachment area between the pelvis and sacrum relative to other basal ornithopods, and a robust, fused scapulocoracoid with a prominent scapular spine. 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 not necessarily washed into 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., 2010). The phylogenetic

position of *Drinker* is not well known, however *Koreanosaurus* was placed in a monophyletic clade with *Oryctodromeus* (Huh et al., 2010), along with *Orodromeus* and *Zephyrosaurus* (Varricchio et al., 2007). Boyd et al. (2009) found that *Thescelosaurus* also belonged in this monophyletic 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 ornithopods vary greatly in size and locomotor style, 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). Figure 3.1 shows the phylogenetic relationship of the taxa examined in this study.

Though burrowing behavior is present in birds and crocodilians, for example, burrowing owls (Thomsen, 1971), Magellanic penguins (Stokes and Boersma, 1991),

blue penguins (Waas, 1990), American alligators (Martin et al., 2012), and Chinese alligators (Cheng-kuan, 1957), these taxa do not provide an adequate analog for osteological specialization for digging. Burrowing birds typically use their hind limbs to dig rather than their forelimbs, whereas burrowing crocodilians often lack any morphological specialization for digging in the forelimbs, whose morphology instead reflects their sprawling posture and semi-aquatic lifestyle (Kley and Kearney, 2007). The osteological correlates of burrowing in mammals, however, have been well described in the literature. Mammals typically use one of three main types of digging: hook-and-pull digging, humeral rotation digging, and scratch-digging. Hook-and-pull digging is not typically used for burrowing, but for food gathering. Adaptations for hook-and-pull digging include enlarged manus claws on the second and third digits and an enlarged medial epicondyle of the humerus, as well as adaptations of the musculature for stronger flexion of claws and forelimb. The adaptations for humeral rotation digging include a cranial shift of the glenoid, horizontally oriented scapula, articulation of the clavicle with the humerus instead of the scapula, and shortened forelimbs. The osteological adaptations for scratch-digging include an expanded posterior angle of the scapula, enlarged medial epicondyle of the humerus, enlarged olecranon process of the ulna, large claws which are either sharp and laterally compressed for loosening soil or broad and blunt for moving soil, and fusion of sacral and pelvic elements for bracing while digging (Hildebrand, 1985).

Whereas the extant phylogenetic bracket (EPB) of *Oryctodromeus* does not provide a suitable framework for analyzing digging morphology, the gross

morphological adaptations for digging in mammals might be an appropriate analog. However, because the morphologies of the forelimb elements vary so widely between dinosaurs and mammals (e.g. prominence of the coracoid in dinosaur pectoral girdle, sternal morphology, glenoid morphology), it is difficult to identify and directly compare homologous structures. Therefore, the forelimbs of *Oryctodromeus* are compared with other ornithischian dinosaurs to quantitatively describe how the forelimbs exhibit morphological specialization. Then these features can be compared with general trends in burrowing mammals to determine whether the specializations in *Oryctodromeus* are consistent with adaptations for digging. Traditional and geometric morphometric analyses are methods by which the forelimb morphology of *Oryctodromeus* can be quantitatively described and compared with that of other ornithopod dinosaurs. Results may show whether the forelimbs of *Oryctodromeus* are outliers of any morphologic trends within Ornithopoda, or if *Oryctodromeus* clustered with other ornithopod taxa. Clustering with *Orodromeus,* the sister taxon to *Oryctodromeus*, or other closely related basal ornithopods, may indicate that they also created burrows, as suggested by Varricchio et al. (2007). Absence of any biologically significant difference in the forelimb of *Oryctodromeus* would argue against any specializations for digging. In this case, the specimens of *Oryctodromeus* found within the burrow structure may have stolen the burrow from another animal, or *Oryctodromeus* may have been able to construct a burrow but lacked specialized forelimb morphology for the behavior, as is seen in some mammals (Hildebrand, 1985).

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 inflection points on elements, and semilandmarks, representing non-homologous points that usually describe the curvature of an element, are superimposed on photographs of elements in order to compare shapes of different specimens (Zelditch et al., 2012). Though 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 in order to more thoroughly describe the forelimb morphologies of several ornithischian taxa.

A total of 73 humeri, 47 scapulae, and 22 coracoids from at least 18 genera of ornithischian dinosaurs (listed in Appendix A) were measured and photographed for the traditional and geometric morphometric analyses. Length measurements of morphological features were used in the traditional morphometric analysis, and morphological landmarks were digitized from photographs for the geometric morphometric analysis. Unlike a phylogenetic analysis, neither traditional nor geometric

morphometric analyses are typically capable of handling missing data, therefore only complete or nearly complete elements could be used in this analysis.

Institutional abbreviations – **NHMUK,** Natural History Museum, London, U.K.; **BYU**, Brigham Young University, Provo, UT; **CM,** Carnegie Museum, Pittsburgh, PA; **DBDP/DBJP**, Utah Geological Survey, Salt Lake City, UT; **FMNH**, Field Museum of Natural History, Chicago, IL; **IMNH,** Idaho Museum of Natural History, Pocatello, ID; **MOR**, Museum of the Rockies, Bozeman, MT; **UMNH**, Utah Museum of Natural History, Salt Lake City, UT; **YPM**, Yale Peabody Museum of Natural History, Yale University, New Haven, CT.

Traditional morphometric analysis

For the traditional morphometric analysis, ten measurements were taken on the humerus, nine on the scapula, and eight on the coracoid of each specimen. Some of the following measurements were modified from and expanded upon Galton's description of *Hypsilophodon* (1974). Measurements greater than 150 mm were taken with a flexible tape measure, measurements less than 150 mm were taken with General UltraTECH calipers.

The traditional morphometric analysis of the humerus included 73 specimens, representing a minimum of 18 identified genera, with some specimens not identified beyond family or subfamily. Ten measurements were used to describe the variation in shape in ornithopod humeri (Table 3.1, Fig. 3.2). The measurements were chosen to describe the most shape variation between the humeri of different genera to provide the most informative results. However it is difficult to describe all shape variation via linear

measurements, therefore certain morphological data is lost, such as the orientation of the deltopectoral crest relative to the orientation of the proximal humerus. In basal ornithopods, the deltopectoral crest expands perpendicular to the proximal humerus, whereas in more derived ornithopods such as hadrosaurs, the deltopectoral crest is more in line with the orientation of the proximal humerus.

The traditional morphometric analysis for scapulae included 47 specimens. This sample included 17 distinct general and several specimen not identified beyond family or subfamily. Nine measurements were used to describe the variation in ornithischian scapulae (Table 3.2, Fig. 3.2). Like in 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.

The traditional morphometric analysis of the coracoid included 22 specimens from 12 distinct genera. Eight measurements were used to describe the variation of ornithopod coracoids (Table 3.3, Fig. 3.2).

After the measurements were compiled, the data was 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 one (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. Then the PCA can be run on either the variance-covariance matrix or the correlation matrix, though 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 (Kambic, 2008; Maloiy et al., 1979). Due to a lack of associated femur material for many specimens in this study, size was accounted for by dividing all other variables by total element length. This allowed comparison of the measurements as a ratio to element size, which are denoted by an “r” subscript. To test for correlation between morphological variation and size, PC scores of significant axes were compared with element size in a linear regression.

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. As 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, 2012). However in some cases corresponding structures cannot be defined, and 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, coracoids were photographed in lateral view, and humeri were photographed in anterior view. With the Thin Plate Spline (TPS) Suite of computer programs these photographs were converted to a TPS file with TPS Utility Program (Rohlf, 2010c), then imported into TPSDig2 (Rohlf, 2010a), where scale and landmark data were superimposed on the photographs.

For the humerus, eight landmarks and ten semilandmarks were used in the analysis (Fig. 3.3). This study includes 58 specimens from 18 distinct genera, and some specimens not identified beyond a family or subfamily level. Seven of the landmarks were inflection points rather than corresponding structures, as 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 landmarks on the humerus describe the following features: (1) medial end 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) distalmost radial condyle, (6) inflection point of the intercondylar groove, (7) distalmost ulnar condyle, and (8) inflection point of the medial epicondyle. The semilandmarks are used to describe the overall shape of the humeral shaft (Fig. 3.3), 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).

A total of 37 scapulae from 16 distinct genera, as well as some specimens not identified beyond the family or subfamily level, were used in the geometric morphometric analysis. In the scapula, there are eight landmarks and 15 semilandmarks (Fig. 3.3). Four of the landmarks are corresponding structures (points 1, 2, 6, and 7); the remaining four are inflection points. The semilandmarks describe the three edges of the scapular blade, with five semilandmarks to describe each edge. The landmarks on the scapula describe the following features: (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, and (8) posterior margin of the deltoid fossa, where the glenoid ridge meets the scapular spine. The semilandmarks describe the overall 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 edge 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 ventralmost edge of the scapular glenoid (6) describe the ventral edge of the scapular blade.

In total, 19 coracoids from 11 distinct genera were used in the geometric morphometric analysis. In the coracoid, there are eight landmarks and six semilandmarks (Fig. 3.3). Three of the landmarks are corresponding structures (points 1, 2, and 3), the remaining five are inflection points. The six semilandmarks describe the curvature of the anterodorsal edge of the coracoid. The landmarks on the coracoid describe the following features: (1) dorsal end of the scapulocoracoid suture, (2) ventral edge of the scapulocoracoid suture, (3) ventral edge of the glenoid, (4) posterior coracoid indentation, (5) anterior coracoid indentation, (6) ventralmost point of sternal process, (7) dorsalmost edge of coracoid foramen, and (8) ventralmost edge of coracoid foramen. The six semilandmarks are used to describe the anterodorsal curve of the coracoid, and are evenly spaced between the dorsal end of the scapulocoracoid suture (1) and the ventralmost point of the sterna process (6).

The landmarks were mathematically described by conducting a relative warp analysis (RWA) using TPS Relative Warps (Rohlf, 2010b), 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 are remove 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 the data to compare the morphological data with discrete phylogenetic groupings using the IMP program CVAGEN6o (Sheets, 2006). DFA tests how well the data can be explained by predefined groups, and whether morphology can be used predictively to determine classification into a group. DFA does this by generating canonical variates which 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.

RESULTS

Traditional Morphometrics

The results for the principal component analysis on the correlation matrix of the raw measurement data for the humerus and scapula indicate that most of the variance is due to the overall size of the element, rather than the 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 therefore is insignificant. In the scapula PC1 describes 92.1% of the variation in the data, and PC2 describes 4.0% of the variation, and is insignificant. In the coracoid, PC1 describes 74.3% of the variation in the data, whereas PC2 describes 12.7% of the variation. All other principal components are insignificant. Due to the 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. As these results correlate with size (for the humerus R^2=0.975; for the scapula R^2=0.981; for the coracoid R^2=0.953), they do not give any shape information, they 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. 3.4). 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 one).

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 (DPL_r) and the ratio of distal humeral width to humeral length (HDW_r). Basal ornithopod humeri produce more positive PC1 values and more derived ornithopods produce more negative PC1 values, which indicate a trend which roughly follows increasing adult body size and change in locomotor style from bipedal to quadrupedal. The ornithopod specimens also exhibit a trend in phylogeny from more basal to more derived within the clade for PC1, however basal ornithischians and marginocephalians are not morphological outliers as one would expect if PC1 were explained primarily by phylogeny. Hadrosaurids, iguanodontian, and marginocephalians all share a PC1 values, though hadrosaurids and iguanodontians exhibit a wider range of PC1 values, and both groups overlapping with values for basal ornithopods. All basal ornithopods have positive PC1 scores except *Haya griva* (FMNH 200/2015) and one specimen of *Hypsilophodon* (BMNH R192), which have slightly negative PC1 scores. 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 a functional significance for 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, as 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 & Wilson 2008).

PC2 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 which are dorsoventrally expanded, whereas more negative values indicate wider proximal and distal ends with a more robust deltopectoral crest and/or shorter distal condyles. PC2 is not influenced by phylogeny, as basal ornithopods, iguanodontians, and hadrosaurids all occupy roughly the same range of PC2 values. Marginocephalians occupy a relatively limited range of PC2 scores, from -3 to -1, and basal ornithischian PC2 scores range from -2 to 1. Specimens of *Oryctodromeus* have moderate PC2 values of between -1 and 1, whereas specimens of *Orodromeus* have only positive PC2 values, which range roughly from 0.5 to 2. *Hypsilophodon* specimens have highly variable PC2 values, ranging from -2 to 4. 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, as individual species, such as *Hypsilophodon foxii* exhibits a wide range of PC2 scores. Much of the variety in PC2 appears to represent deformation of the humerus during preservation and fossilization.

PC3 is explained primarily by the 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. PC3 appears to have significance outside of size or phylogenetic relationship (Fig. 3.5). Linear regression shows no evidence supporting a linear correlation between body size and PC3 score (R^2=0.1512). Phylogenetic relationship does not strongly correlate with PC3 as hadrosaurs have positive PC3 values, and basal ornithopods and iguanodontians have negative PC3 values. However, *Oryctodromeus* stands out from other basal ornithopods in that the specimens, excepting one (MOR 1636), have more strongly positive PC3 scores than other basal ornithopods, scoring similarly to some hadrosaurs. Specimens of the Late Cretaceous *Orodromeus* exhibited a high variability in PC3 scores, ranging from -2.5 to 0.

Scapula – In the traditional morphometric analysis of the scapula, when all measurements are a ratio of scapular length, the first two principal components are significant (Fig. 3.6). The first two principal components explain a cumulative 73.9% of

the variation in scapular morphology (PC1 explains 58.5%, PC2 explains 15.4% of the variation).

PC1 is influenced by the dorsoventral expansion of the scapula relative to its length, being positively correlated with the anterior width of the scapula (SAW_r), length of the scapulocoracoid articulation ($SCAL_r$), height of the posterior margin of the scapular blade (PBW_r), and the minimum height of the scapular blade (MBL_r), and minorly with the length of the scapular spine (SSL_r), and slightly negatively correlated with the distance to the superior angle of the scapular blade (SAL_r), distance to the inferior angle of the scapular blade (IAL_r) and length of the scapular blade (BL_r), all relative to scapular length. As seen in Figure 3.5, specimens of *Oryctodromeus* have strongly positive PC1 values, ranging from 5 to 6, whereas other basal ornithopods have lower PC1 scores ranging from 0 to about 3. Iguanodontian and marginocephalian specimen score near zero or negative for PC1, and hadrosaurid specimens have consistently negative PC1 scores. Basal ornithischians exhibit a large range of PC1 scores, with *Lesothosaurus* scoring highly negatively, *Stormbergia* scoring slightly positively, and *Othnielosaurus* scoring positively with a score similar to specimens of *Hypsilophodon* and *Orodromeus*. There is no support that PC1 correlates with body size even when juvenile specimens are removed (R^2=0.0896). PC1 does appear to correlate with phylogeny, however as there is a trend of hadrosaurs with strongly negative PC1 scores, iguanodontian scores with negative scores, basal ornithopods with positive scores. However, *Oryctodromeus* and basal ornithischians are outliers in this phylogenetic trend, as *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: quadrupedal ornithischians exhibiting negative PC1 scores, and bipedal ornithischians with more positive PC1 scores.

PC2 is influenced strongly by BL_r, and IAL_r, and weakly by SAW_r, and $SCAL_r$. Longer scapular blades relative to the total length of the scapula would result in strongly positive PC2 values, where 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. PC2 shows no correlation with body size, even when juvenile specimens are removed (R^2=0.0158).

Coracoid – In the traditional morphometric analysis of the coracoid, the first three principal components explain 75.1% of the variation in morphology (PC1 explains 42.1%, PC2 explains 18.7% and PC3 explains 14.3%). The graphical results of the traditional morphometric analysis of the coracoid can be seen in Figure 3.7.

PC1 is explained primarily by coracoid maximum height (CH_r), coracoid minimum height (CMH_r), and scapulocoracoid articulation length ($SCAL_r$), all as ratios with coracoid length. As with PC1 of the scapula, PC1 of the coracoid is explained by the dorsoventral expansion relative to the coracoid length. Negative PC1 scores indicate a more strongly dorsoventrally expanded coracoid relative to the length, whereas positive

PC1 scores indicate a dorsoventrally compressed coracoid relative to the length. Basal ornithopods exhibit scores ranging from -3 to about zero, whereas iguanodontians have PC1 scores ranging from about zero to 3. Only one hadrosaurid coracoid was measured in this analysis, however it produces the greatest PC1 value. Marginocephalian specimens have a PC1 core of about 1 to 2, whereas the two basal ornithischian specimens greatly vary from one another. PC1 scores appear to have a roughly phylogenetic and strongly locomotor signature, with bipedal groups such as basal ornithopods and basal ornithischians having tall coracoids (negative PC1 scores), and more quadrupedal groups such as iguanodontians and marginocephalians with relatively shorter coracoids (positive PC1 scores). However small sample sizes of the groups make it difficult to make any inference, as it is unclear if the full range of morphospace for taxa are displayed. The two *Oryctodromeus* coracoids examined have highly disparate PC1 scores, which is likely due to individual variation or taphonomic effects – *Oryctodromeus* specimen MOR1642 is more dorsoventrally compressed relative to the coracoid length and relative to the other specimen of *Oryctodromeus*, MOR1636. PC1 is not correlated with size (R^2=0.116).

PC2 is explained by the distance of the coracoid foramen from the scapulocoracoid suture ($CFPe_r$) as well as the size of the sternal process of the coracoid relative to the coracoid length (SPH_r). Positive values indicate the coracoid has a small sternal process with the coracoid foramen close to the scapulocoracoid suture whereas negative values indicates the presence of a more pronounced sternal process and coracoid foramen further from the scapulocoracoid suture. *Camptosaurus* specimens (UMNH

VP16422, YPM 1800, YPM 1877, and *Stormbergia* have high PC2 values, where *Haya griva*, one specimen of *Hypsilophodon*, *Protoceratops*, and *Corythosaurus* have low PC2 values. There is no evidence of a linear correlation between PC2 scores and size (R^2=0.211).

PC3 explains the variation in coracoid morphology due to the position of the coracoid foramen ($CFPe_r$ and $CFPa_r$) and length of the scapulocoracoid suture ($SCAL_r$) relative to the length of the coracoid versus the size of the sternal process (SPH_r) and the width of the indentation between the sternal process and the coracoidal glenoid (CIW_r). A positive score indicates a pronounced sternal process, and typically a coracoid foramen located close to a relatively short scapulocoracoid suture. Of course, an extremely pronounced singular trait can overshadow others, such as in *Protoceratops* (CM 9185), which has a strongly positive PC3 score, due to the large sternal process with a wide indentation between the glenoid and sternal process, despite the fact that the coracoid foramen is not located very close to the scapulocoracoid suture relative to other taxa. A negative PC3 score indicates a coracoid foramen far from the ventral scapulocoracoid suture, and a relatively small sternal process positioned close to the glenoid. Despite its pronounced sternal process, *Oryctodromeus* (MOR 1636) has a strongly negative PC3 value due to the position of the coracoid foramen distal to the scapulocoracoid suture, and the close positioning of the glenoid and sternal process. There appears to be no phylogenetic signal in PC3 as iguanodontians, basal ornithopods, and marginocephalians all span the range of PC3 scores, and size is not correlated with PC3 scores (R^2=0.0113).

Geometric Morphometrics

Humerus – The geometric morphometric analysis of the humerus indicates that only the first two relative warp axes (RW) are significant, together explaining 77.01% of the variation in shape. As seen in Figure 3.8, RWA of the humerus indicates that basal ornithopods, iguanodontians, and hadrosaurs roughly separate out from one another, though 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 of the humerus and size of the humerus (which is used roughly to estimate relative body size) are not linearly correlated.

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 score consistent with other basal ornithopods, though 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* (UofC LHVP2) due to the difference in deltopectoral crest length. Basal ornithischians exhibit similar scores to basal ornithopods, falling entirely within the same RW1 range.

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 reduction 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 hadrosaurids 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, $p=9.14 \times 10^{-10}$; 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. 3.9). The CV1 separates groups based on the length of the deltopectoral crest relative to the humeral length, with more negative scores indicating a shorter deltopectoral crest relative to humeral length. 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. 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 CV2 with phylogeny among basal ornithopods, iguanodontians, and hadrosaurs, though *Oryctodromeus* does not follow this trend. Basal ornithischians and marginocephalians have scores similar to basal ornithopods and iguanodontians. CV2 does not show any phylogenetic trend, with all ornithopods except *Oryctodromeus* scoring similarly. CV3 shows a slight separation of basal ornithopods, including *Oryctodromeus,* and more the more derived iguanodontians and hadrosaurs. Specimens of *Oryctodromeus* grouped separately from other basal ornithopods in CV1 and CV2. In CV1 specimens of *Oryctodromeus* are separated morphologically from other basal ornithopods by iguanodontians, whereas in CV2 specimens of *Oryctodromeus* have more strongly positive scores than all other groups. CV3 scores for *Oryctodromeus* are equivalent to other basal ornithopods. 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, though *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, indicating that overall

Oryctodromeus does vary from other basal ornithopods in that it has more medially placed, anteriorly projecting deltopectoral crest, and a relatively longer deltopectoral crest.

Scapula – The geometric morphometric analysis of the humerus indicates that RW1 and RW2 are the only significant axes, explaining 70.89% of the variation in shape. The plot of RW1 vs. RW2 (Fig. 3.10) shows that scapular morphology of ornithopods separates out phylogenetically, though there is some overlap in iguanodontian morphology and basal ornithopod morphology. However, the most striking aspect of the plot is the extreme separation of specimens of *Oryctodromeus* from the other taxa, showing a highly unique morphology. Though 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.

RW1 accounts for 57.48% of the shape variation in the scapula. RW1explains the variation in shape as the dorsoventral 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. Hadrosaurid 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. Specimens of *Oryctodromeus* scapulae 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.

RW2 accounts for 13.50% of the shape variation and describes the rotation of anterior region relative to the scapular blade, positive values indicate 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 3.11) indicated that there were four significant canonical variates in explaining the morphology of the scapula (CV1, $p=5.55 \times 10^{-16}$; CV2, $p=2.67 \times 10^{-7}$; CV3, p=0.0031; CV4, p=0.031). CV1 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. CV2 is explained by the posteroventral expansion of the scapular blade, with positive values indicating a more strongly posteroventral expanded scapular blade. CV3 is explained by the orientation of the anterior scapula and scapulocoracoid articulation, where a positive

value indicates am anteroventrally facing scapulocoracoid articulation and negative values indicate an anterior facing scapulocoracoid articulation. CV4 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 phylogenetic trend (Fig. 3.11). 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. CV2, CV3 and CV4 have no phylogenetic signal. 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.

Coracoid – In the geometric morphometric analysis of the coracoid, the first four relative warp axes are significant, explaining a cumulative 79.60% of the shape variation. RW1 describes 38.18% of the variation in shape, RW2 describes 19.29% of the variation, RW3 describes 11.79% of the variation, and RW4 describes 10.35% of the variation. 93.32% of the variation remains unexplained when centroid size of each element has been regressed against the relative warp scores, indicating that coracoid morphology is not correlated with element, and presumably, body size. No clear trends are evident in the geometric morphometric analysis of the coracoid (Fig. 3.12), which may perhaps be influenced by the small sample size overall, and the limited sample sizes of some groups, such as marginocephalians, basal ornithischians, and *Oryctodromeus*, which each have

two samples. The absence of hadrosaurid coracoid specimens also makes inferences about trends in phylogeny and locomotion difficult.

RW1 is explained by size of the coracoid indentation and sternal process, where a more positive score indicates a larger sternal process with a deep coracoid indentation, and a negative score indicates a shorter sternal process with shallow coracoid indentation. Marginocephalians exhibit a large discrepancy in RW1 scores, as *Protoceratops* (CM 9185) has a positive RW1 score, indicating a large sternal process, whereas *Psittacosaurus* (UofC LHVP2) has a strongly negative RW1 score, indicating a small sternal process. All other taxa represented in this study exhibited moderate to large sternal processes, yielding slightly negative to positive RW1 scores. There is no phylogenetic or locomotor trend evident in RW1 scores.

RW2 describes variation in shape due to the dorsoventral expansion of the coracoid. Positive values indicate a tall coracoid relative to the anteroposterior length, and negative values indicate a relatively shorter coracoid relative to the anteroposterior length. Marginocephalians exhibit strongly negative RW2 scores, indicating short coracoids relative to the anteroposterior length. Basal ornithopods, basal ornithischians, and iguanodontians all exhibit large variation in RW2 scores, indicating that outside of marginocephalians, coracoid morphology does not strictly trend with phylogeny or locomotion.

RW3 describes the proximity of the coracoid foramen to the scapulocoracoid articulation. Negative scores indicate the foramen sits close to the scapulocoracoid articulation, whereas positive scores indicate that a larger distance separates the coracoid

foramen from the scapulocoracoid articulation. Basal ornithopods have positive RW3 scores, indicating a foramen further removed from the scapulocoracoid suture, whereas iguanodontians and basal ornithischians have a larger range of RW3 scores, ranging from slightly positive to strongly negative. Marginocephalians have RW3 scores close to zero, indicating a moderate coracoid foramen position relative to the scapulocoracoid articulation. With the absence of hadrosaurids, it is difficult to determine whether there is any association between RW3 and phylogeny or locomotion.

RW4 is explained by a shift in the position of the coracoid foramen anteroventrally. Positive scores RW4 produce a coracoid with the foramen positioned more ventrally, and distal from the scapulocoracoid articulation, whereas and negative RW4 scores describe a coracoid with the foramen position at a more dorsal position (but still ventral to the midpoint of the coracoid), and positioned proximal to the scapulocoracoid articulation. Basal ornithischians and *Oryctodromeus* have positive RW scores, whereas other basal ornithopods and marginocephalians have RW4 scores close to zero. Iguanodontians have scores ranging from positive to strongly negative. Unlike in the humerus and scapula, the geometric morphometric analysis of the coracoid does not follow any phylogenetic, size, or locomotor trend.

The CVA (Fig. 3.13) indicated that there were three significant canonical variates in explaining the morphology of the coracoid (CV1, $p=0.00048$; CV2, $p=0.0046$; CV3, $p=0.031$). CV1 explains the position of the coracoid foramen and the width of the indentation between the coracoidal glenoid and the sternal process. Positive values indicate a wider indentation and a more anteriorly placed coracoid foramen. CV2

describes the size of the sternal process and the depth of the indentation, with positive values indicating a smaller sternal process and a shallower indentation between the glenoid and sternal process. CV3 describes the size of the coracoid indentation and the height of the scapulocoracoid articulation, with positive values indicating a narrower indentation between the glenoid and sternal process and a taller scapulocoracoid articulation. CV1 may potentially trend with phylogeny with iguanodontians having negative CV1 scores and basal ornithopods having positive CV1 scores, however the small sample sizes, as well as the lack of hadrosaurid specimens makes it difficult to ascertain. Iguanodontians span the range of CV2 scores, however basal ornithopods have negatve CV2 scores, *Oryctodromeus* has scores near zero, and marginocephalians and basal ornithischians have positive CV2 scores. CV3 does not separate out into morphologically disparate groups. The only coracoid specimen that is misclassified in an *a posteriori* test of the groupings is one iguanodontian that is misclassified as a basal ornithischian.

DISCUSSION

Morphological Trends

Humerus –The morphospace of iguanodontians, basal ornithopods, and hadrosaurids overlap in PC1 and PC2 and RW1 and RW2 (Figs. 3.4, 3.8, 3.9). Basal ornithopods typically score at one end 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 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 indicate that most of the shape variation in humeral morphology is correlated with locomotor style, which also correlates with phylogeny. Positive PC1 scores and negative RW1 scores correlate with the bipedality of basal ornithopods. Only *Koreanosaurus* is described as quadrupedal (Huh et al., 2010), and it was not included in this study, so its position in the morphospace is unknown. Negative PC1 scores and positive RW1 scores are associated with hadrosaurs, which were likely quadrupedal at slow speeds and while resting (Fastovsky and Weishampel, 2005). The overlap in the scores of the ornithopod groups may reflect the gradation of Ornithopod phylogeny, as basal ornithopods and iguanodontians are both paraphyletic grades (Butler et al., 2008). PC2 and RW2 are likely represent a taphonomic influence, with strongly positive and negative scores indicating distortion due to compression of the bones. Overall, Most of the variation in ornithopod forelimbs results from the length of the deltopectoral crest relative to the humeral length, as well as the overall robustness of the humerus. PC3 shows a separation of humeri to more gracile humeri with lower scores, and more robust humeri with positive scores (Fig. 3.5). In this axis, hadrosaurids and *Oryctodromeus* exhibit more strongly positive scores than basal ornithopods and iguanodontians. The CVA shows a deviation from the phylogenetic trend seen in the PCA and RWA, indicating that when between group variance is maximized, *Oryctodromeus* scores differently from other basal ornithopods, separated by iguanodontians indicating the variance explained does not follow a phylogenetic trend for CV1 or CV2 (Fig. 3.9).

In the first two axes of the PCA and RWA, *Oryctodromeus* scores within the ranges present in basal ornithopods, indicating the humeral morphology is not significantly different, though they do fall on the more extreme ends of the ranges. The third principal component of the PCA indicates however that the humerus of *Oryctodromeus* is slightly more robust than that of other basal ornithopods. Despite the PCA revealing only a slight difference between *Oryctodromeus* and other basal ornithopods, and the RWA showing no difference, the CVA shows that *Oryctodromeus* is distinct from other basal ornithopods in CV1 and CV2. The CV1 score of *Oryctodromeus* indicates a longer the deltopectoral crest relative to other basal ornithopods and the CV2 score indicates 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, variation in scapular morphology is primarily described by the 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. In the all three analyses the most variation in scapular morphology, which is described by the first axes (PC1, RW1, and CV1), is explained by the dorsoventral expansion of the scapula, at both the acromion and the posterior scapular blade, and shows a roughly phylogenetic trend (Figs. 3.6, 3.10, 3.11). 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. 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. The traditional morphometric analysis is less consistent with mode of locomotion as an explanatory factor, because *Lesothosaurus* (BMNH RU B.17) and specimens of *Psittacosaurus,* both bipedal, have similar PC1 scores to the more quadrupedal hadrosaurids and iguanodontians. Overall, scapular morphology does not correlate with element size, but superficially trends with phylogeny, with *Oryctodromeus* as an outlier from other basal ornithopods.

Oryctodromeus has a strongly positive score in 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 scapula. 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 as 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. Though 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.

Coracoid – Overall, the variation in coracoid shape is primarily controlled by the dorsoventral height of the coracoid relative to its anteroposterior length, the size of the sternal process, and the position of the coracoid foramen relative to the scapulocoracoid articulation (Figs. 3.7, 3.12, and 3.13). However, no trend associated with any particular function is evident, though the CVA of the coracoid shows that when between-group variance is maximized, there is a rough separation of basal ornithopods from iguanodontians, indicating a weak relationship with phylogeny. As there is only one hadrosaurid specimen in the PCA and none included in the RWA, it is not possible to determine if any stronger phylogenetic or locomotor trend in ornithopod coracoids is evident. Marginocephalians fall out separately from basal ornithischians and all ornithopod groups in the RWA. The sternal process of the coracoid, and the indentation between the sternal process and glenoid, which describe together much of the shape variation in ornithopod coracoids, act as the origin site for the coracobrachialis brevis muscle (Maidment and Barrett, 2011), and the insertion of the sternocoracoideus or costocoracoideus superficialis muscle respectively (Dilkes, 2000). However, overall it appears that the coracoid morphology was relatively conservative throughout the phylogeny of Ornithopoda, indicating that its function remained similar throughout ornithopod phylogeny and may not have been seriously impacted by the transition from bipedal to quadrupedal or functional specialization. Specimens of *Oryctodromeus* fall within the range the scores of other basal ornithopods and the shape does not appear to represent any specialization relative to other ornithopods.

General Morphological Trends – Overall, the humeral and scapular morphology of ornithopod dinosaurs appears to trend with phylogeny, which is correlated with locomotor mode. The humeri of more derived ornithopods exhibit longer, laterally expanded deltopectoral crests, and the scapulae are narrower and more strap-like. Basal ornithopods exhibit gracile humeri with shorter, anteriorly projecting deltopectoral crests and dorsoventrally expanded scapulae. Increasing quadruepdality and increasing body size were likely driving forces behind the morphological change of the forelimb elements through ornithopod phylogeny, however due to the nature of the specimens chosen – some undescribed, and some not identified to a species or even genus level – it was impossible to generate a phylogenetic tree of the specimens with which to analyze the morphometrics results statistically. Therefore the relationship between phylogeny, locomotion and morphology still remains relatively unexplained.

Morphological Specialization of *Oryctodromeus* – The humerus of *Oryctodromeus* differs slightly from that of other basal ornithopods. Relative to more derived ornithopods, basal ornithopods have short deltopectoral crests that expand anteriorly, though 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 in digging, such as the pectoralis, supracoracoideus, and deltoideus (Dilkes, 2000; Maidment and Barrett, 2011). Thus deltopectoral crest morphology is important in understanding the functional morphology of the humerus, as

a larger deltopectoral crest would allow for greater muscle attachment area, which leads to larger muscles, and stronger muscle action.

Unlike the humerus, the scapula of *Oryctodromeus* is clearly distinct from all other 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.

The examined coracoids of *Oryctodromeus* exhibit a large range of scores in the morphometric analyses, but still score within the range of other basal ornithopods. Due to the use of only two specimens in the RWA and CVA, no clear morphospace can be defined for *Oryctodromeus*, which hinders any potential interpretation of any specialization for *Oryctodromeus.* With what little resolution is available, the coracoid of *Oryctodromeus* does not appear specialized relative to other ornithopods for any function.

Implications for Digging

As previously mentioned, there are three primary types of forelimb digging used within mammals: the hook-and-pull method, the humeral rotation method, and scratch-digging method. The osteological evidence recognized here for *Oryctodromeus* appears most consistent with scratch-digging as the method of constructing burrows. Adaptations for hook-and-pull burrowing 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 manus claws is unknown, as 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 adaptations for scratch-digging are most consistent with the features seen in *Oryctodromeus.* The scapula of *Oryctodromeus* differs greatly from other basal ornithopod 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 deltoideus clavicularis and supracoracoideus (Maidment and Barrett, 2011). The broadly expanded scapular blade would have increased the surface area of the broad origin of the deltoideus scapularis (Maidment and Barrett, 2011), a muscle important in digging in mammals (Hildebrand, 1985). The musculature of *Oryctodromeus* is further explored in

the following chapter of this volume. The humerus is only slightly adapted for digging, as the medial condyle of the humerus is not expanded 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 coracoid does not appear to be specialized for any digging or other purpose, and remains morphologically conservative throughout ornithopod phylogeny.

Limitations of this Study

Though the evidence does seem to support the presence of adaptation beneficial for digging in *Oryctodromeus*, it is important to note that relative to the levels of inference (Witmer, 1995), the comparison of *Oryctodromeus* to mammals is a level III inference. Level III inferences imply a high degree of uncertainty when reconstruction soft tissue adaptations for behaviors. However this high degree of uncertainty is inevitable, as the extant phylogenetic bracket of *Oryctodromeus* does not contain examples of archosaurs with adaptations for digging, it is of little help in this morphometric analysis. The forelimb morphology of mammals and archosaurs, though grossly homologous, proves difficult to compare directly to one another, as 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 like foxes and dogs (Hildebrand, 1985) is

considered, the presence of any morphological specialization beneficial for 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 on the humerus, as it utilizes the third dimension more fully than the relatively flat scapula and coracoid. However, the lack of proper equipment necessitated the use of two-dimensional geometric morphometrics instead. The use of traditional morphometrics is limited by the fact overall shape data can be lost when just taking a series of measurements, as there is no way to know how 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, as 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 morphometrics analysis is also hindered by the small sample sizes, within individual taxa and overall. The results for the coracoid seem most impacted by small sample sizes, as no informative results were obtained from the morphometric analyses of the coracoids.

CONCLUSION

The morphometric analyses showed that ornithopod morphology trends with mode of locomotion. Larger quadrupedal ornithopods have a more strap-like scapula and 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.

Though the potential for digging within dinosaurs has only recently begun to be explored (Bakker, 1996; Senter, 2005; Senter, 2007; Varricchio et al., 2007; Martin, 2009; Simpson et al., 2010; Fowler and Hall, 2010; Huh et al., 2010), the most compelling evidence for digging in dinosaurs is *Oryctodromeus*, which is supported by both strong taphonomic evidence (Varricchio et al., 2007; Woodruff and Varricchio, 2011), and the morphological evidence presented both here and in the original description of *Oryctodromeus* (Varricchio et al., 2007). Though the coracoid does not appear to bear specialization 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* bears the greatest specialization of the elements, 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. Though not analyzed in this study, the ulnae of *Oryctodromeus* do not appear specialized for digging, as the olecranon process is short.

Despite the limitations of this study, useful morphological information can be gained by morphometric analyses. Both the traditional and geometric morphometric analysis provided consistent summaries of the morphospace of ornithopod forelimbs,

indicating that there was not a severe loss of morphological data. Though the lack of analogs for digging in the EPB make inference about digging more difficult, generalizations about digging adaptations can be made with some certainty. The relative robustness of the humerus of *Oryctodromeus*, as well as the expanded acromion process and posterior blade margin of the scapula both point to adaptations for scratch-digging. Further study into the impact of these osteological features and their interaction with soft-tissue is examined in the forelimb musculature reconstruction of *Oryctodromeus* (Chapter 4, this volume).

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TABLES

Table 3.1. Humerus measurements for the traditional morphometric analysis. Refer to Figure 3.1

Humeral length	HL	the distance from the proximalmost to distalmost humerus
Deltopectoral crest length	DPL	the length from the head of the humerus to the apex of the deltopectoral crest
Deltopectoral crest width	DPW	the width of the deltopectoral crest at its apex.
Humeral head width	HHW	the width of the proximal end of the humerus anteroposteriorly
Humeral proximal width	HPW	the width of the proximal end of the humerus transversely
Humeral shaft width	HSW	the transverse width of the humeral shaft at its narrowest
Humeral shaft width (perpendicular)	HSP	the width of the humeral shaft perpendicular to HSW
Humeral distal width	HDW	the width of the distal end of the humerus transversely
Radial condyle width	RCW	the width of the radial/lateral condyle anteroposteriorly
Ulnar condyle width	UCW	the width of the ulnar/medial condyle anteroposteriorly

Table 3.2. Measurements used in the traditional morphometric analysis of the scapula. Refer to Figure 3.2 for these measurements for *Oryctodromeus*.

Scapular length	SL	the anteroposterior length of the scapula from the midpoint of the scapulocoracoid suture to the midpoint of the posterior edge of the blade.
Scapular blade length	BL	length of the blade parallel to the SL from the midpoint of the posterior edge of the scapular bade to the intersection of the scapular spine and glenoid ridge.
Scapular spine length	SSL	the length of the scapular spine from the end of the acromion process to the junction with the glenoid ridge
Scapular anterior width	SAW	the width of the scapula from the acromion process to the ventralmost edge of the glenoid
Minimum blade width	MBW	the minimum dorsoventral width of the scapular blade
Posterior blade width	PBW	the width of the scapula from the superior angle to the inferior angle of the scapular blade
Scapulocoracoid articulation length	SCAL	the length of the suture between the scapula and the coracoid
Superior angle length	SAL	the length from the ventral edge of the scapulocoracoid suture to the superior angle
Inferior angle length	IAL	the length from the ventral edge of the scapulocoracoid suture to the inferior angle

Table 3.3. Description of coracoid measurements for the traditional morphometric analysis. Refer to Figure 3.3.

Coracoid length	CL	the maximum length of the coracoid perpendicular to the scapulocoracoid suture
Coracoid height	CH	the height of the coracoid from the dorsalmost edge to the tip of the coracoidal glenoid
Coracoid minimum height	CMH	the height of the coracoid from the dorsalmost edge to the indentation posterior to sternal process
Coracoid indentation width	CIW	the width from the edge of the coracoid glenoid to the ventralmost part of the sternal process
Sternal process height	SPH	the length of the ventral expansion of the sternal process relative to the indentation posterior to it
Coracoid foramen-perpendicular	CFPe	the distance perpendicular to the scapulocoracoid suture to the coracoid foramen
coracoid foramen-parallel	CFPa	the distance from the ventralmost scapulocoracoid suture to the coracoid foramen, parallel to the suture
Scapulocoracoid articulation length	SCAL	the length of the suture between the scapula and the coracoid

FIGURES

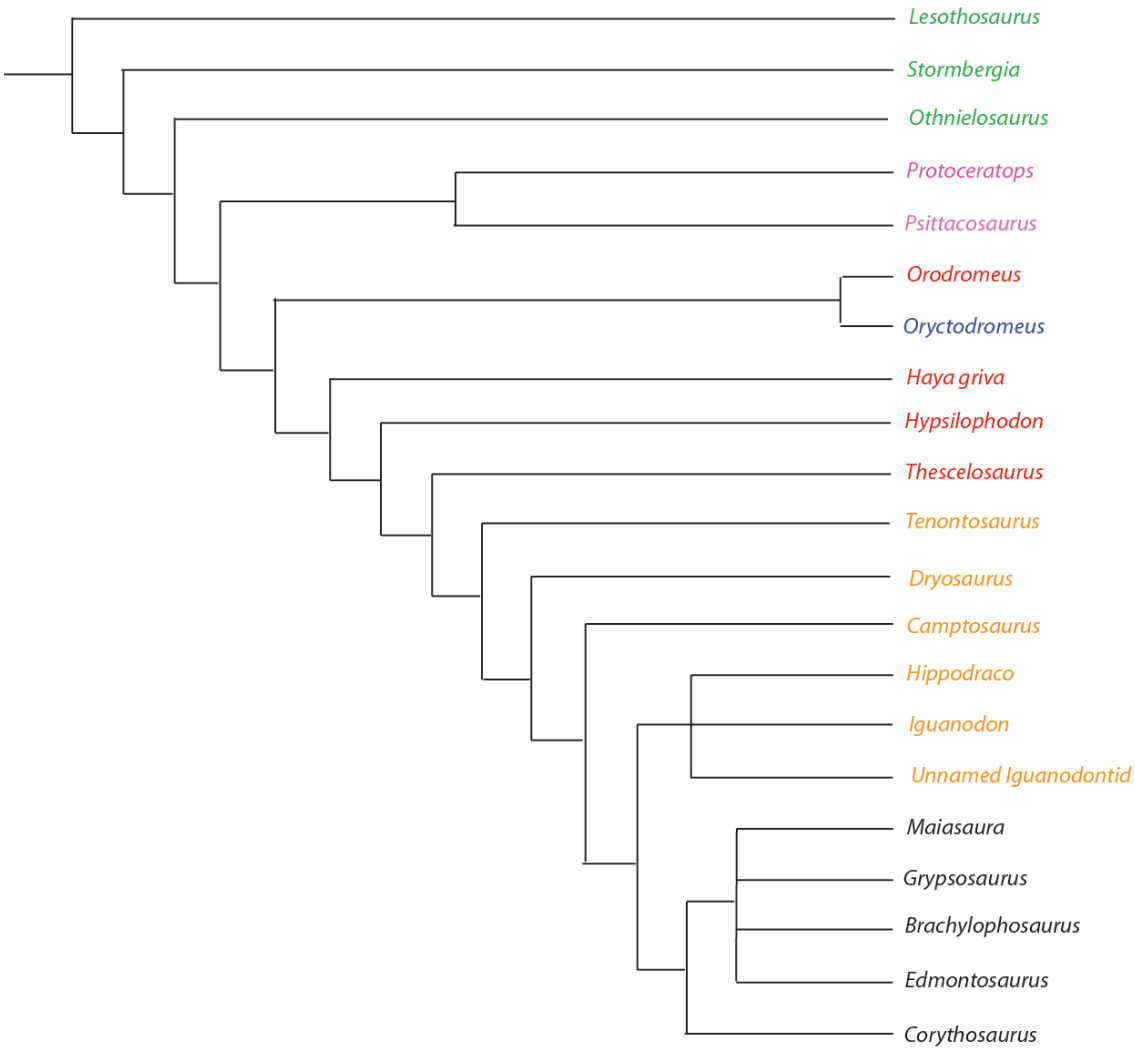

Figure 3.1. A cladogram of the genera used in this analysis. Some genera listed are represented by multiple species, or by specimens of indeterminate species, and some specimens in this study were only identified to the family or subfamily level (such as "hadrosaur" or "lambeosaur"). Color-coding is based on the separation of groups for the statistical analyses; basal ornithischians are green, marginocephalians are pink, basal ornithopods (except *Oryctodromeus*) are red, *Oryctodromeus* is blue, iguanodontians are orange, and hadrosaurids are black. This tree was compiled using relationships from several sources (Varricchio et al., 2007; Butler et al., 2008; McDonald et al., 2010; and Makovicky et al., 2011).

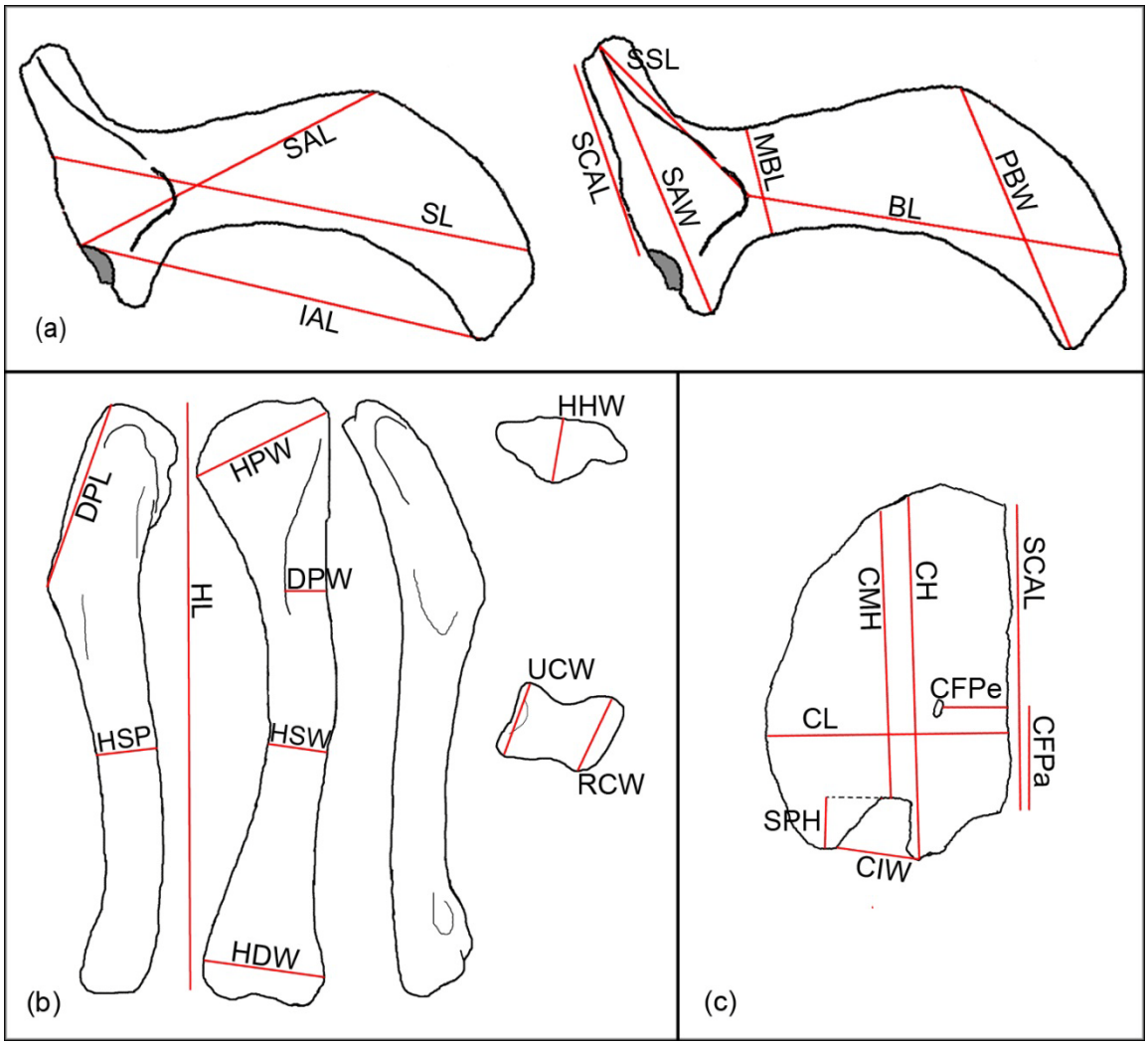

Figure 3.2. The measurements used in the traditional morphometric analysis, described in more detail in Tables 3.1-3.3, for (a) the scapula in lateral view, (b) the humerus in lateral, anterior, medial, proximal and distal views, and (c) the coracoid in lateral view.

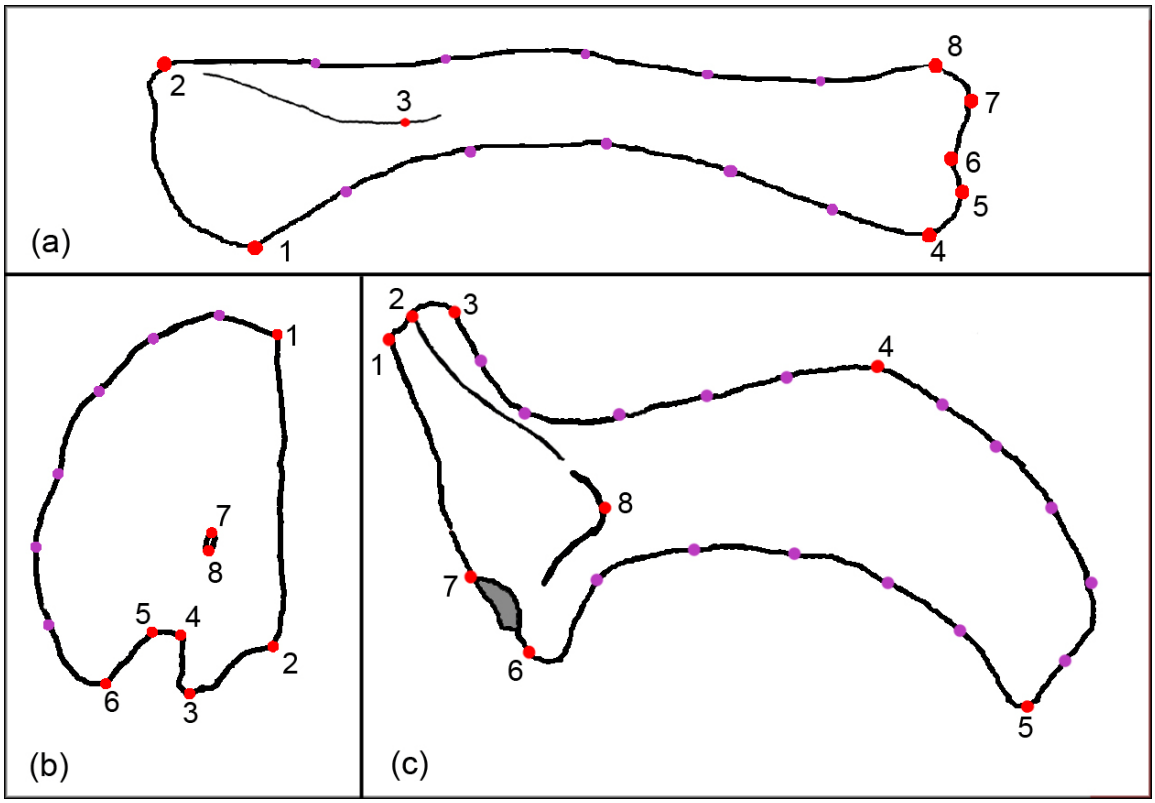

Figure 3.3. Landmark and semilandmark locations for the geometric morphometric analysis of the (a) humerus in anterior view, (b) coracoid in lateral view, and (c) scapula in lateral view. Landmarks are in red, semilandmarks in purple.

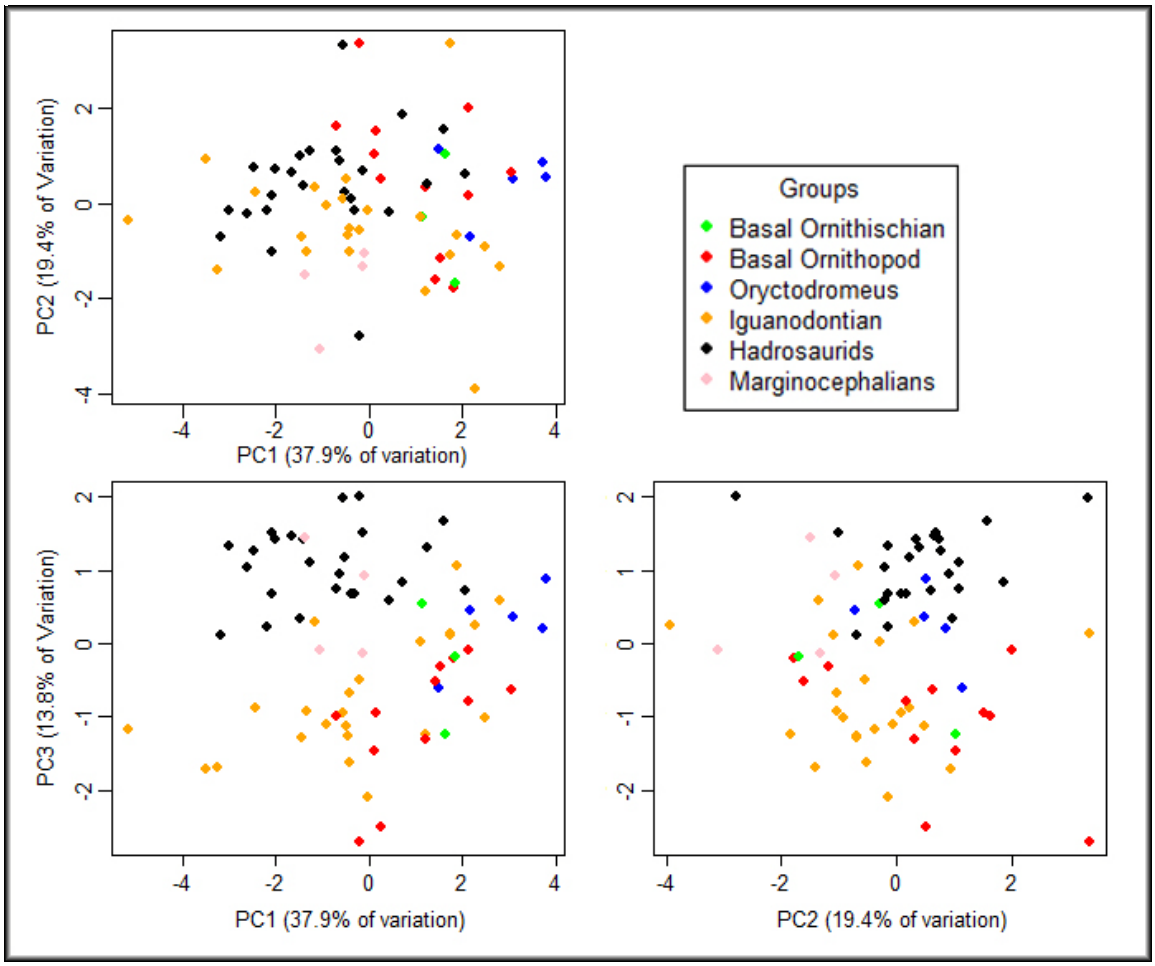

Figure 3.4. Traditional morphometrics PCA results for the humerus. PC1 and PC2 do not show any separation between *Oryctodromeus* and other basal ornithopods. However in PC3, *Oryctodromeus* specimens have positive scores while other basal ornithopods have negative scores, indicating a slightly more robust humerus in *Oryctodromeus*.

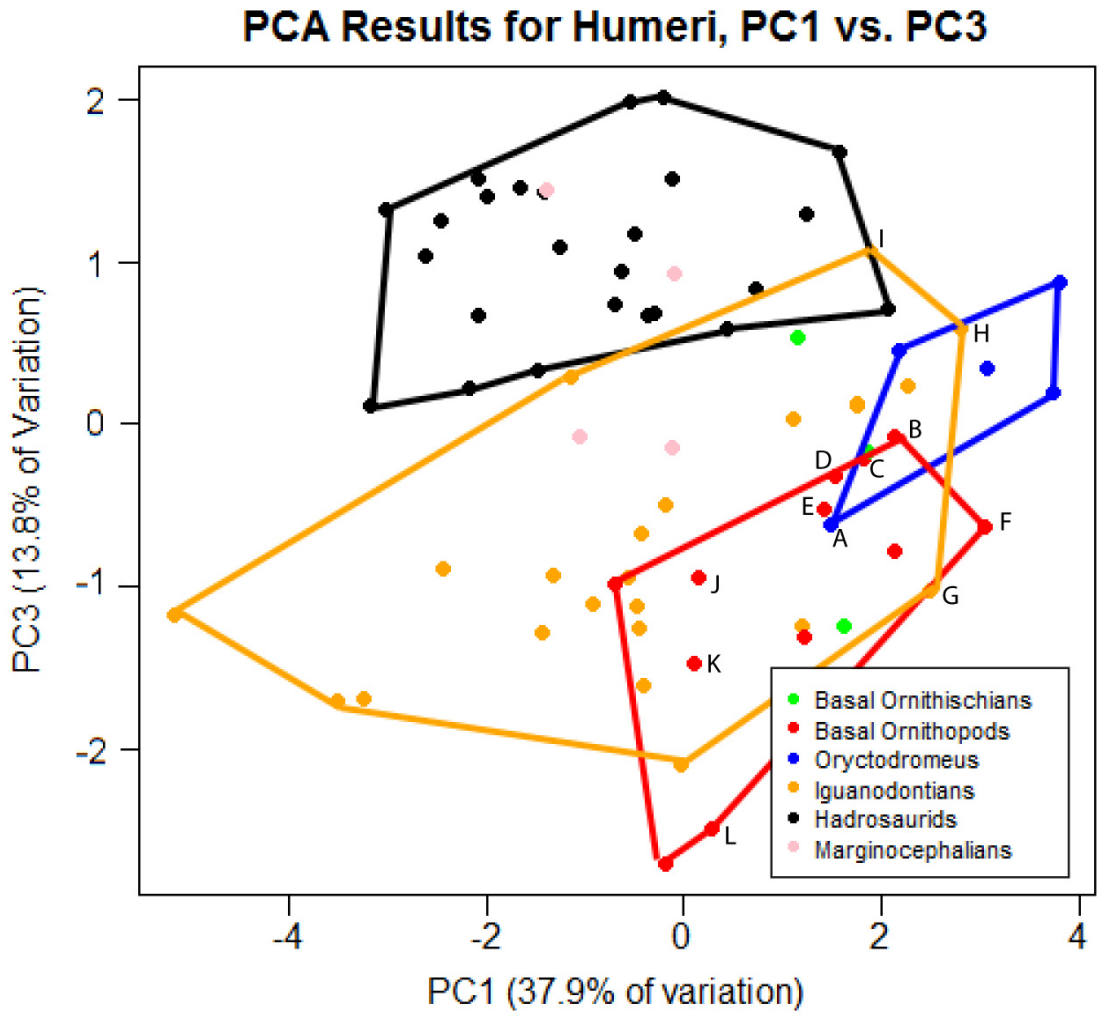

Figure 3.5. PCA of the humerus, PC1 vs. PC3. Specimens of *Oryctodromeus* have higher PC3 scores than other basal ornithopods. Labeled specimens are: A. *Oryctodromeus* (MOR 1636), B, J-L. *Orodromeus* (MOR 623, MOR 473, MOR 294, MOR 404), C-D, F. *Hypsilophodon* (BMNH R196, R192), E. *Thescelosaurus* (CM 9900), G-H. *Dryosaurus* (CM 21786, BYU 5215), I. Iguanodontian indet. (DBDP-42).

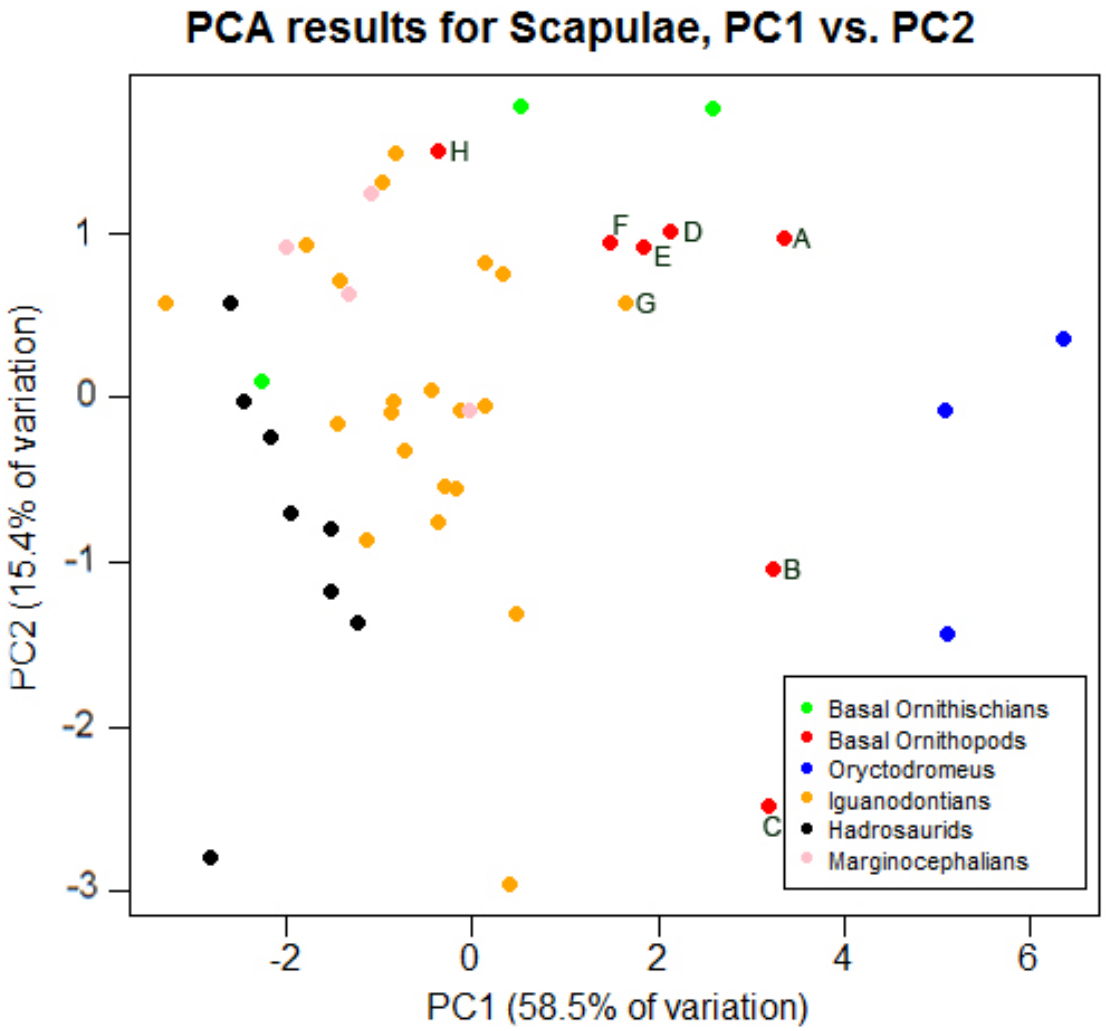

Figure 3.6 Traditional morphometrics PCA results for the scapula. *Oryctodromeus* scores strongly positively in PC1, forming a group distinct from other ornithopods. A.Hypsilophodontid indet. (UMNH VP20644), B, D, H. *Hypsilophodon* (BMNH R196, BMNH R196, BMNH R192), C & F. *Orodromeus* (MOR 623, MOR 294), E. *Haya* (FMNH IGM 100/2015), G. *Tenontosaurus* (MOR 628).

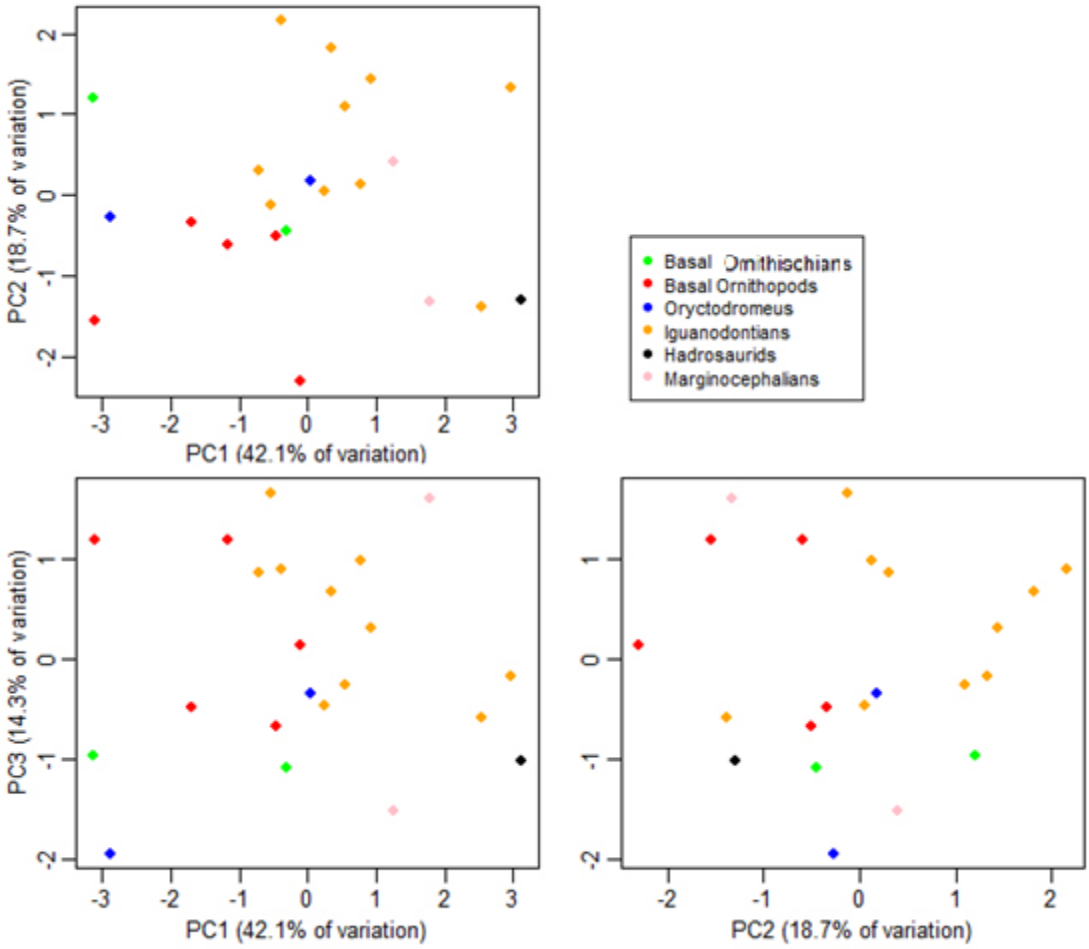

Figure 3.7. PCA results for the traditional morphometric analysis of the coracoid. *Oryctodromeus* specimens show a broad range of scores, given the small sample size. MOR 1636 is has a strongly negative PC1 and PC3 score, while MOR 1642 scores near zero in all three principal components.

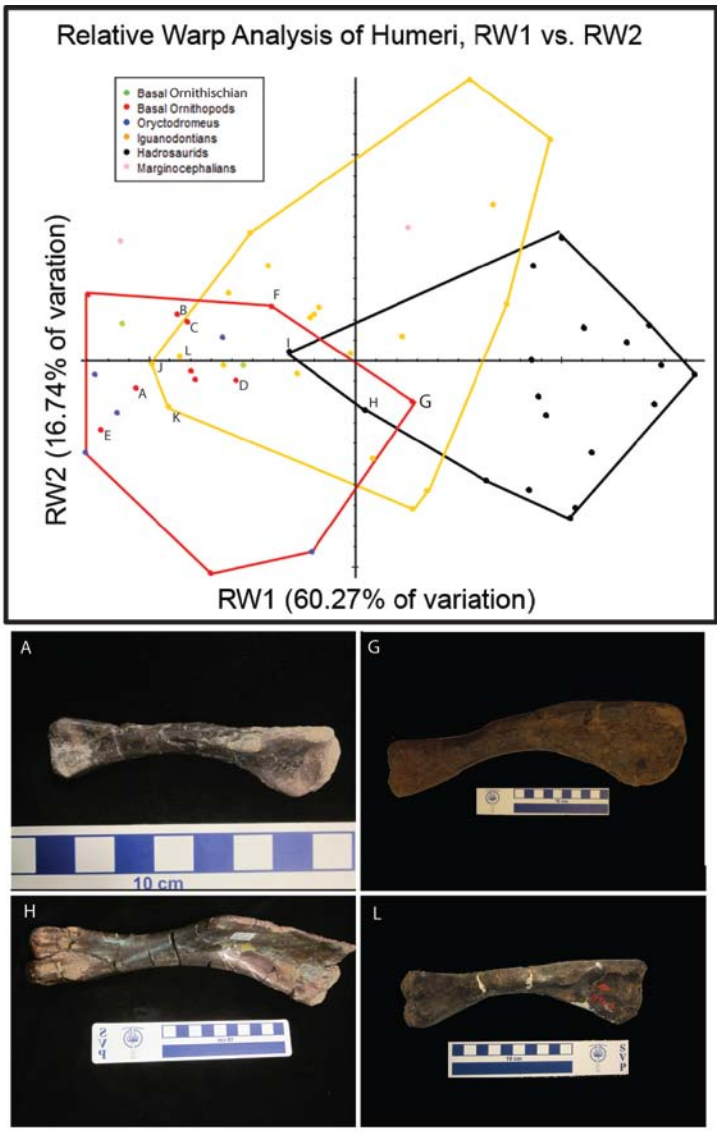

Figure 3.8. The first two relative warp axes of the geometric morphometric analysis of the humerus, which shows a trend of larger, quadrupedal, derived ornithopods on the right, and small, basal, bipedal ornithopods on the left. specimens of *Oryctodromeus* group with other basal ornithopods. A-D. *Orodromeus* (MOR 404, MOR 623, MOR 473, 294), E. *Hypsilophodon* (BMNH R196), F-G. *Thescelosaurus* (MOR HC-164, CM 9900), H. *Maiasaura* (MOR 547a) I. “Hadrosaur indet.” (CM 1066), J-L. *Dryosaurus* (CM 21786, CM 3392, YPM 1876).

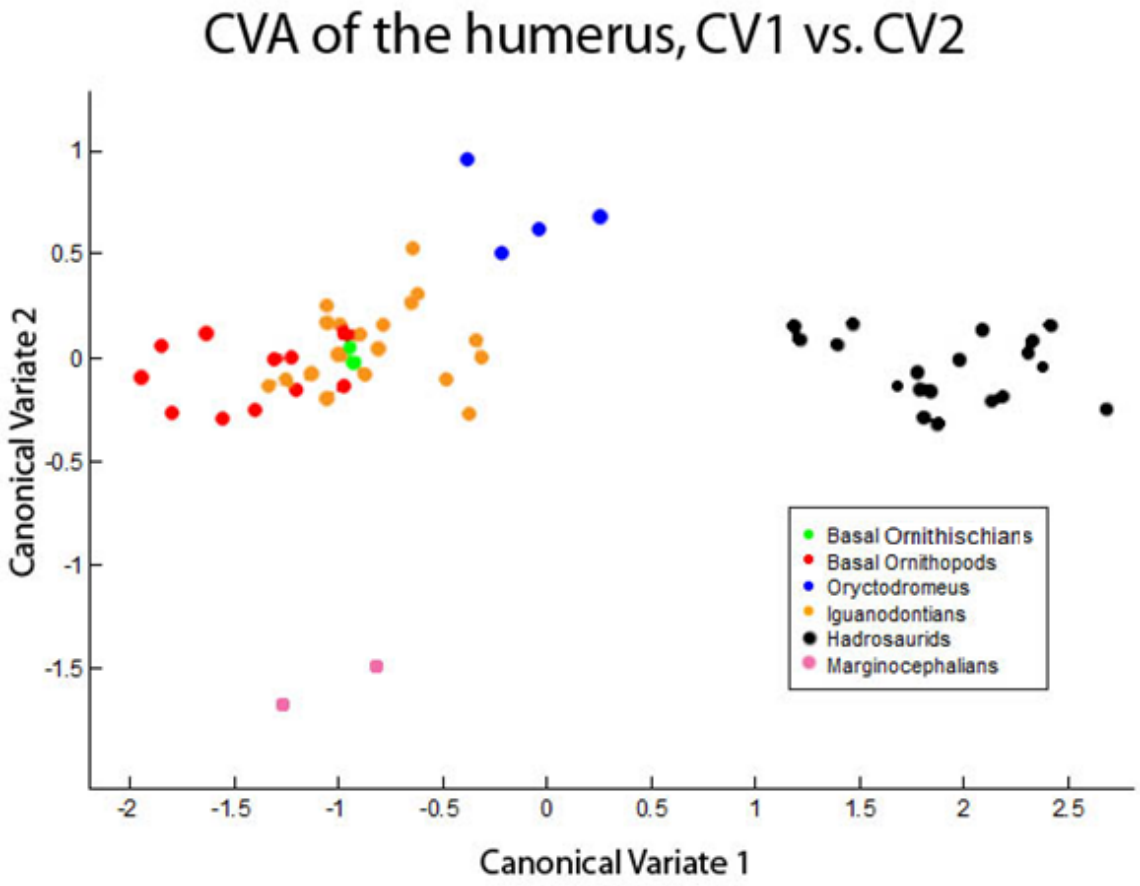

Figure 3.9. Canonical variates analysis of the humerus. The different phylogenetic groupings sort out very distinctly, with the exception of the overlap between basal ornithopods (excluding *Oryctodromeus*), iguanodontians, and basal ornithischians.

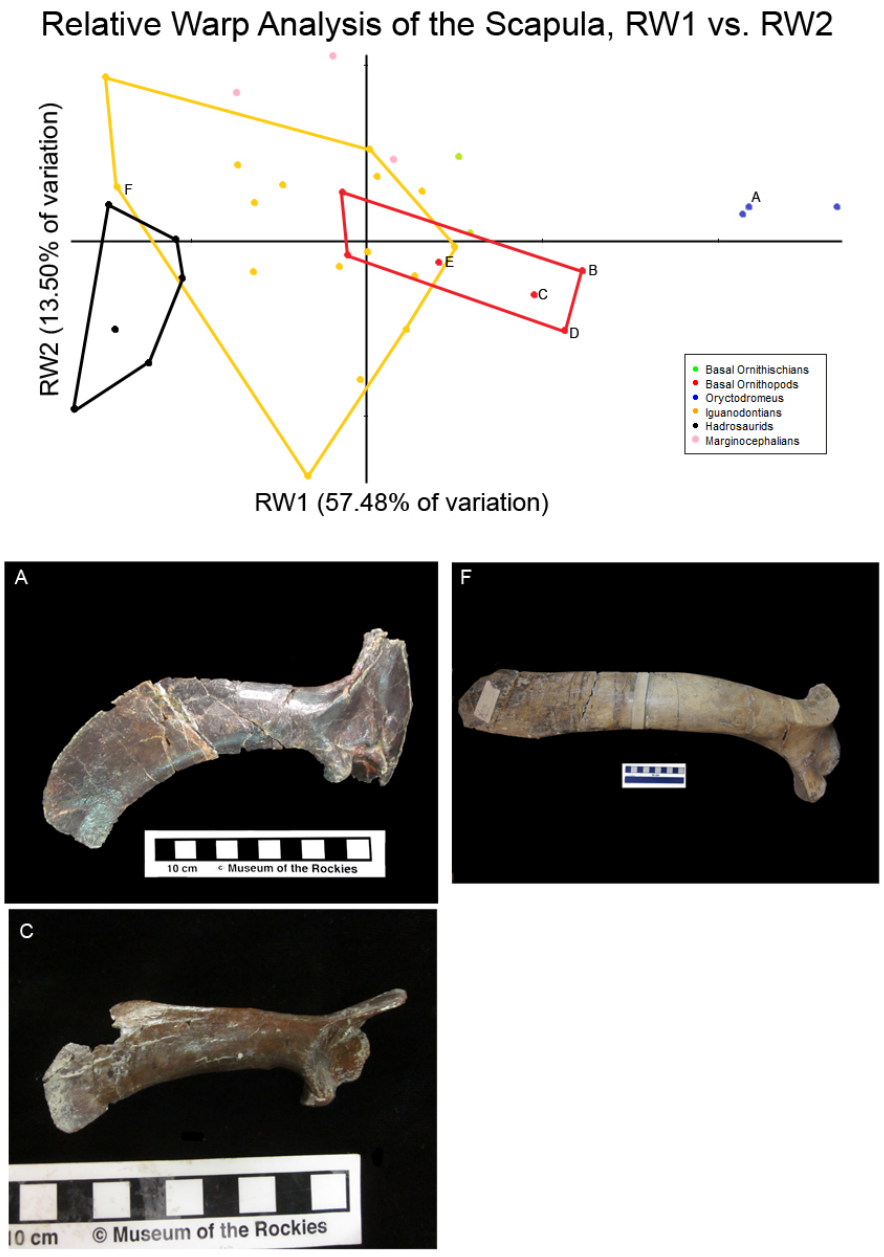

Figure 3.10. The first two relative warp axes for the geometric morphometric analysis of the scapula. This graph indicates that the scapular morphology of *Oryctodromeus* is distinct from other basal ornithopods, with strongly positive scores. A. *Oryctodromeus* (MOR 1636), B. *Haya* (FMNH IGM 100/2015), C & E. *Orodromeus* (MOR 623, MOR 294), D. *Hypsilophodon* (BMNH R196), F. *Iguanodon* (BMNH R2196).

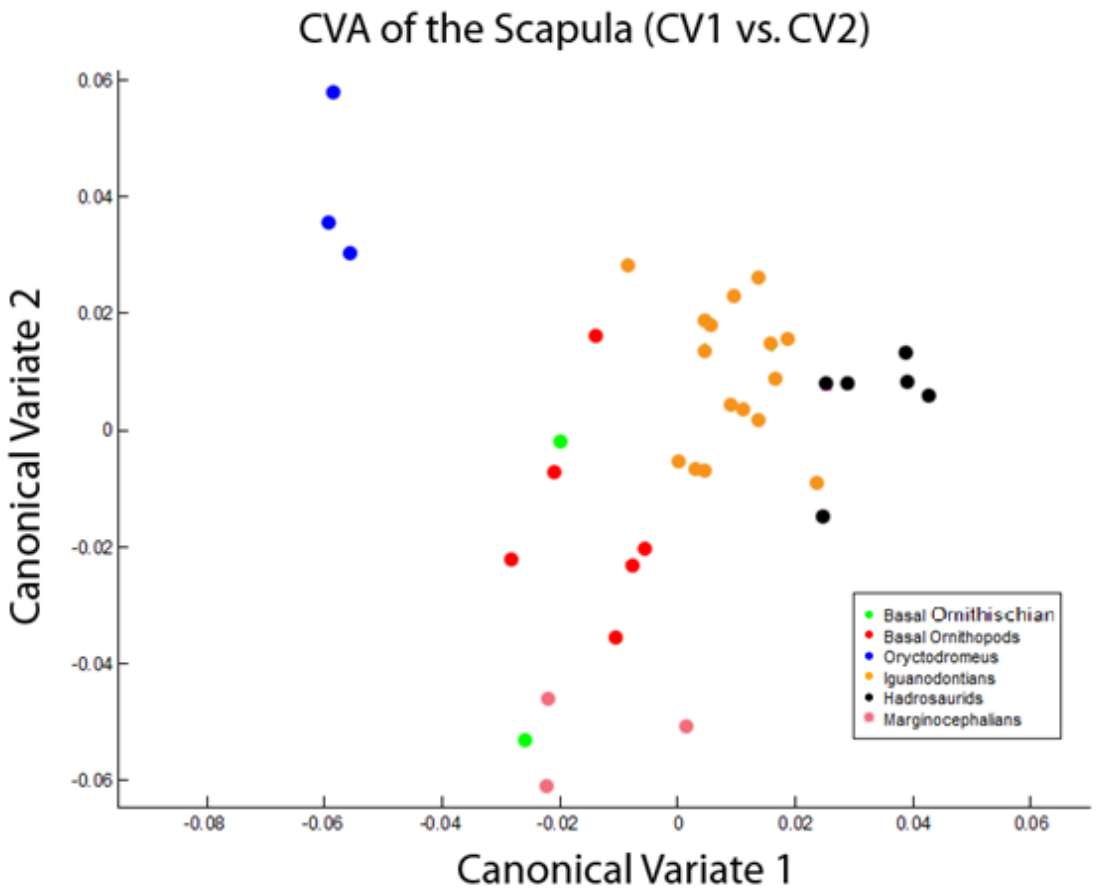

Figure 3.11. CVA of the Scapula. Oryctodromeus is distinct from basal ornithopods, but otherwise the groups within Ornithopoda sort out phylogenetically.

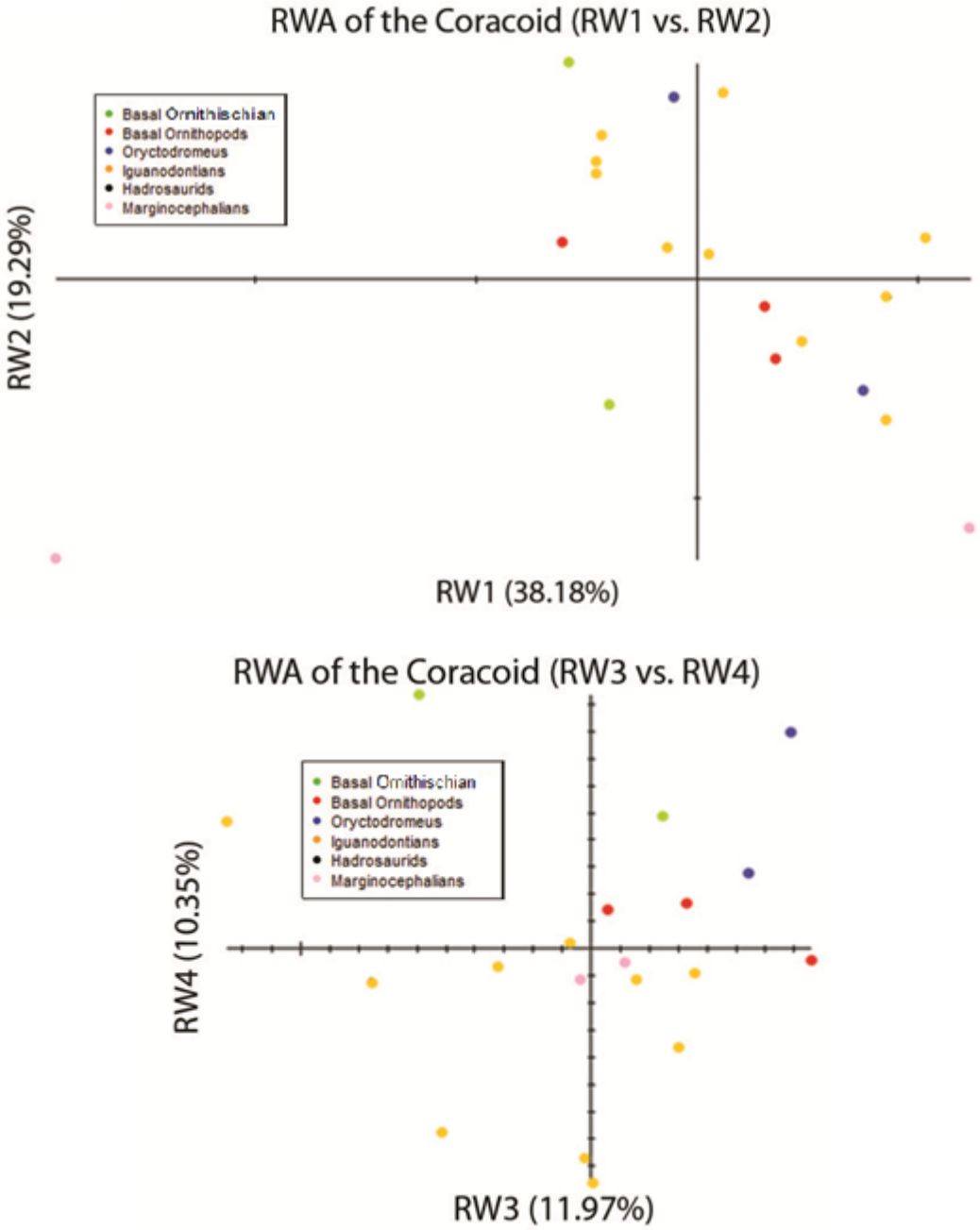

Figure 3.12. Relative warp analysis results for the coracoid. (A)RW1 vs. RW2 for the geometric morphometric analysis of the coracoid. (B) RW3 vs. RW4 for the geometric morphometric analysis of the coracoid.

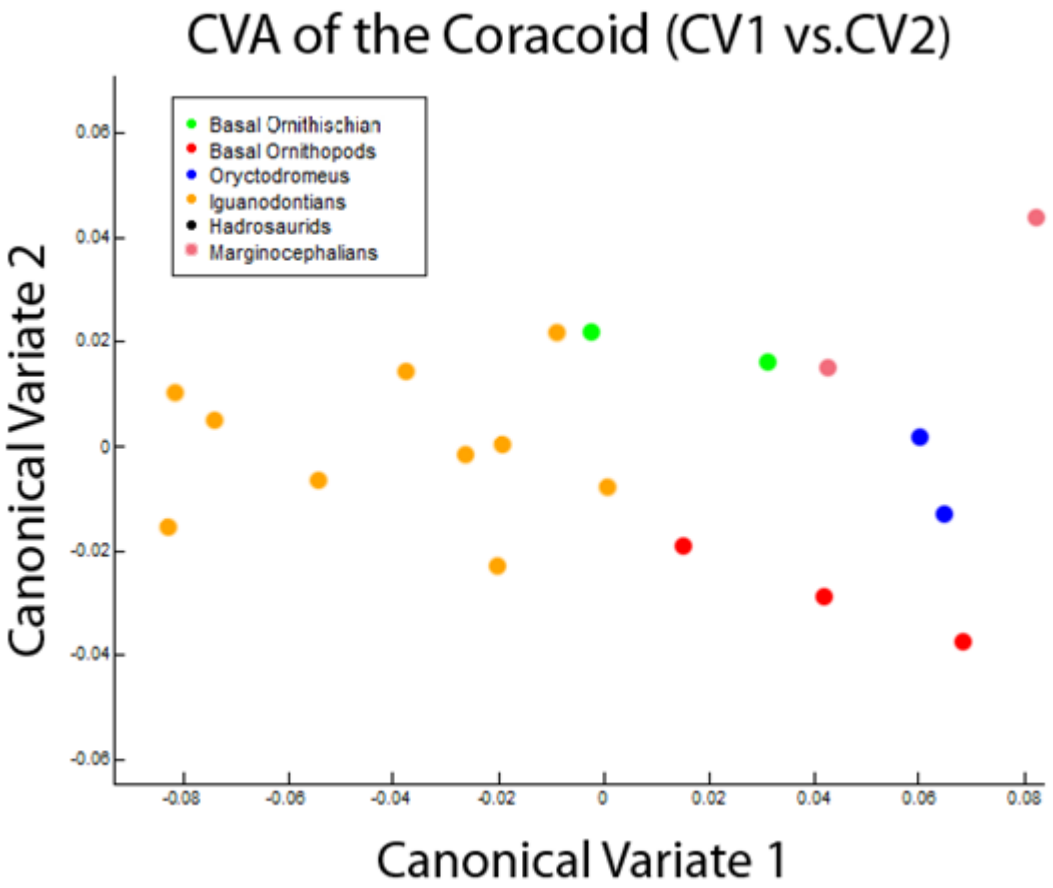

Figure 3.13. CVA of the coracoid. A phylogenetic signal is difficult to ascertain due to the low number of specimens, however iguanodontians have negative scores and basal ornithopods, including *Oryctodromeus* have positive scores.

REFERENCES

Bakker, R. T. 1996. The real Jurassic park: dinosaurs and habitats at Como Bluff, Wyoming. The Continental Jurassic: Museum of Northern Arizona Bulletin 60:35–49.

Boyd, C. A., C. M. Brown, R. D. Scheetz, and J. A. Clarke. 2009. Taxonomic revision of the basal neornithischian taxa *Thescelosaurus* and *Bugenasaura*. Journal of Vertebrate Paleontology 29:758–770.

Butler, R. J., P. Upchurch, and D. B. Norman. 2008. The phylogeny of the ornithischian dinosaurs. Journal of Systematic Palaeontology 6:1–40.

Carpenter, K., and Y. Wilson. 2008. A new species of *Camptosaurus* (Ornithopoda: Dinosauria) from the Morrison Formation (Upper Jurassic) of Dinosaur National Monument, Utah, and a biomechanical analysis of its forelimb. Annals of Carnegie Museum 76:227–263.

Cheng-kuan, C. 1957. Observations on the life history of Chinese alligator (*Alligator sinensis fauvel*). Acta Zoologica Sinica 2:004.

Dilkes, D. W. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. Transactions-Royal Society of Edinburgh 90:87–125.

Fastovsky, D. E., and D. B. Weishampel. 2005. Ornithopods. The Evolution and Extinction of the Dinosaurs, 2nd ed. Cambridge University Press, pp. 186-218.

Fowler, D. W., and L. E. Hall. 2010. Scratch-digging sauropods, revisited. Historical Biology 23:27–40.

Galton, P. M. 1974. The Ornithischian Dinosaur Hypsilophodon from the Wealden of the Isle of Wight. British Museum (Natural History).

Hammer, Ø., and D. A. T. Harper. 2005. Paleontological Data Analysis, 1st ed. Wiley-Blackwell, pp. 83-91.

Hildebrand, M. 1985. Digging of quadrupeds. Functional Vertebrate Morphology 89–109.

Horner, J. R., D. B. Weishampel, and C. A. Forster. 2004. Hadrosauridae. The Dinosauria 2:438–463.

Huh, M., D. G. Lee, J. K. Kim, J. D. Lim, and P. Godefroit. 2010. A new basal ornithopod dinosaur from the Upper Cretaceous of South Korea. Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 259:1–24.

Kambic, R. E. 2008. Multivariate analysis of avian and non-avian theropod pedal phalanges. Montana State University Bozeman.

Kley, N. J., and M. Kearney. 2007. Adaptations for Digging and Burrowing; in Fins into limbs: evolution, development, and transformation. University of Chicago Press, pp. 284–309.

Maidment, S. C. R., and P. M. Barrett. 2011. The locomotor musculature of basal ornithischian dinosaurs. Journal of Vertebrate Paleontology 31:1265–1291.

Makovicky, P. J., B. M. Kilbourne, R. W. Sadleir, and M. A. Norell. 2011. A new basal ornithopod (Dinosauria, Ornithischia) from the Late Cretaceous of Mongolia. Journal of Vertebrate Paleontology 31:626–640.

Maloiy, G. M. O., R. Alexander, R. Njau, and A. S. Jayes. 1979. Allometry of the legs of running birds. Journal of Zoology 187:161–167.

Manly, B. F. J. 2005. Multivariate Statistical Methods: A Primer, Third Edition, 3rd ed. Chapman and Hall/CRC, pp. 105-124.

Martin, A. J. 2009. Dinosaur burrows in the Otway Group (Albian) of Victoria, Australia, and their relation to Cretaceous polar environments. Cretaceous Research 30:1223–1237.

Martin, A.J., M. Page, R.K. Vance, and S. Skaggs. 2012. Dens of the American alligator (*Alligator mississippiensis*) as traces and their predictive value for finding large archosaur burrows in the geologic record. Society of Vertebrate Paleontology: Program and Abstracts, 136.

McDonald, A.T., J.I. Kirkland, D.D. DeBlieux, S.K. Madsen, J. Cavin, A.R.C. Milner, L. Panzarin. 2010. New basal iguanodonts from the Cedar Mountain formation of Utah and the evolution of thumb-spiked dinosaurs. PLoS ONE 5(11).

Norman, D. B. 2004. Basal Iguanodontia. The Dinosauria 2:413–437.

R Development Core Team. 2010. R Version 2.11.1 Available at http://www.r-project.org/

Rohlf, F.J. 2010a. TPSDig. Version 2.16. Available at http://life.bio.sunysb.edu/morph/

Rohlf, F.J. 2010b. TPS Relative Warps. Version 1.49. Available at http://life.bio.sunysb.edu/morph/

Rohlf, F.J. 2010c. TPS Utility Program. Version 1.46. Available at http://life.bio.sunysb.edu/morph/

Senter, P. 2005. Function in the stunted forelimbs of Mononykus olecranus (Theropoda), a dinosaurian anteater. Paleobiology 31:373.

Senter, P. 2007. Analysis of forelimb function in basal ceratopsians. Journal of Zoology 273:305–314.

Sereno, P. C. 2010. Noasaurid (Theropoda: Abelisauroidea) skeleton from Africa shows derived skeletal proportions and function. Society of Vertebrate Paleontology: Program and Abstracts, 162A.

Sheets, H.D. 2000. CoordGen6h. Available at http://www3.canisius.edu/~sheets/morphsoft.html

Sheets, H.D. 2006. CVAGen6o. Available at http://www3.canisius.edu/~sheets/morphsoft.html

Simpson, E. L., H. L. Hilbert-Wolf, M. C. Wizevich, S. E. Tindall, B. R. Fasinski, L. P. Storm, and M. D. Needle. 2010. Predatory digging behavior by dinosaurs. Geology 38:699.

Stokes, D. L., and P. D. Boersma. 1991. Effects of substrate on the distribution of Magellanic Penguin (*Spheniscus magellanicus*) burrows. The Auk 923–933.

Thomsen, L. 1971. Behavior and ecology of burrowing owls on the Oakland Municipal Airport. The Condor 73:177–192.

Varricchio, D. J., A. J. Martin, and Y. Katsura. 2007. First trace and body fossil evidence of a burrowing, denning dinosaur. Proceedings of the Royal Society B: Biological Sciences 274:1361–1368.

Waas, J. R. 1990. An analysis of communication during the aggressive interactions of little blue penguins (*Eudyptula minor*). Penguin Biology 345–373.

Woodruff, D. C., and D. J. Varricchio. 2011. Experimental modeling of a possible *Oryctodromeus cubicularis* (Dinosauria) burrow. Palaios 26:140–151.

Zelditch, M. L., D. L. Swiderski, and H. D. Sheets. 2012. Geometric Morphometrics for Biologists, Second Edition: A Primer, 2nd ed. Academic Press.

CHAPTER FOUR

RECONSTRUCTION OF THE FORELIMB MUSCULATURE OF THE CRETACEOUS ORNITHOPOD DINOSAUR *ORYCTODROMEUS CUBICULARIS*: IMPLICATIONS FOR DIGGING

Contribution of Authors and Co-Authors

Manuscripts in Chapters 3 and 4

Author: Jamie L. Fearon

Contributions: Obtained grants, collected and analyzed data, wrote manuscript.

Co-Author: David J. Varricchio

Contributions: Collected a majority of *Oryctodromeus* specimens, provided significant edits to grant proposals and manuscripts.

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Reconstruction of the forelimb musculature of the Cretaceous ornithopod dinosaur *Oryctodromeus cubicularis*: implications for digging

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ABSTRACT – Taphonomic and morphological evidence suggests that *Oryctodromeus cubicularis*, a basal ornithopod dinosaur from the mid-Cretaceous of Montana, constructed burrows by digging with their forelimbs. Reconstruction of the forelimb musculature of *Oryctodromeus* was carried out using the extant phylogenetic bracket method, with crocodilians and ratites as the extant analogs, aided by the presence of osteological correlates and comparison with other ornithopod dinosaurs. Though reconstructions directly from the extant phylogenetic bracket are relatively conservative, the reconstruction elucidates several potential adaptations for burrowing. The prominent muscle groups used in burrowing in mammals are the deltoideus, teres major, latissimus dorsi, and triceps longus. In *Oryctodromeus* the deltoideus scapularis, and equivocally the teres major, have broad origins on the distal scapular blade, which would produce strong muscle action. Neither the origins of the deltoideus scapularis nor the teres major produce osteological correlates in extant taxa or *Oryctodromeus*, however the ventrally expanded posterior scapular blade would have increased attachment area for the origin of these muscle groups. The presence of the latissimus dorsi is supported by the extant phylogenetic bracket, but produces no osteological correlates in *Oryctodromeus*. The triceps longus originates posterior to the glenoid and inserts on the ulna. Due to the proximity of the triceps longus origin to the glenoid, the triceps longus likely did not

provide strong muscle action. As many mammals and reptiles produce burrows without any morphological specialization, the limited but beneficial specializations associated with digging present may sufficiently support adaptation for burrowing in *Oryctodromeus.*

INTRODUCTION

Oryctodromeus cubicularis is a hypsilophodontid grade ornithopod dinosaur (Varricchio et al., 2007). The holotype and paratype material were discovered in a preserved burrow structure in the mid Cretaceous Blackleaf Formation of Montana (Varricchio et al., 2007). This taphonomic evidence, as well as the presence of osteological features potentially beneficial in digging such as fused premaxillae, robust pelvis, and fused scapulocoracoid with unique morphology, led to the hypothesis that *Oryctodromeus* constructed dens using the forelimbs, potentially for raising young and escaping predators (Varricchio et al., 2007).

Morphometric analyses indicate that the scapula of *Oryctodromeus* was morphologically distinct from other basal ornithopods, with a taller, narrow acromion process and a strongly posteroventrally expanded scapular blade (this text, chapter 3). These characteristics follow the morphological trend present in other basal ornithischians, which exhibit a slight ventral expansion of the scapular blade. Other basal ornithopods exhibit some posteroventral expansion of the scapular blade, including *Orodromeus makelai* (Scheetz, 1999) and *Haya griva* (Makovicky et al., 2011). *Thescelosaurus* exhibits a relatively large range of scapular morphology: Parks (1926) describes only a slight posteroventral expansion of the scapular blade, whereas Gilmore (1915) describes a strongly ventral expansion. Morphometric analyses also indicate that the humerus of

Oryctodromeus varies slightly from other basal ornithopods, The humeri of basal ornithopods have narrow proximal and distal ends, and an anteriorly oriented deltopectoral crest which extends less than half the length of the humerus. In more derived ornithopods, the proximal end typically widens and the deltopectoral crest is oriented laterally, and extends about half the length of the humerus. Specimens of *Oryctodromeus* are slightly more robust than other basal ornithopods, with a more prominent, anteromedially oriented deltopectoral crest. These features of the scapula and humerus likely evolved for larger muscle attachment area and therefore greater force for the muscle action. Thus, an analysis of the forelimb musculature associated with these osteological features can elucidate functional significance of the shape of the scapula and humerus in *Oryctodromeus*.

The presence of osteological correlates, features on the bone that indicate the presence of a muscular or tendinous attachment, can help to describe the presence and position of muscle groups. Tendinous, and especially aponeurotic attachment sites were most likely to be preserved than direct muscle attachment sites, though neither type was likely to preserve the entire extent of the attachment (Bryant and Seymour, 2005). Osteological correlates are more prominent in mammals than in birds and reptiles (Bryant and Seymour, 2005). In the weka (*Gallirallus australis*), a flightless carinate, only about 30% of the forelimb muscles were associated with osteological correlates (McGowan, 1986), whereas in *Canis* and *Ursus* about 80% of muscles were associated with osteological correlates (Bryant and Seymour, 2005). Both studies advised caution when basing musculature reconstructions for extinct vertebrates on osteological correlates.

Because of the limited application of osteological correlates in reconstructing soft tissue, the extant phylogenetic bracket (EPB) is commonly used to understand the soft tissue anatomy of extinct taxa (Bryant and Russell, 1992; Witmer, 1995). Different levels of inference for soft tissue structures are assigned based on the presence or absence of these features in the most closely related extant groups. For dinosaurs, the most common taxa used for an EPB analysis are crocodilians and ratites (e.g. Nicholls and Russell, 1985; Dilkes, 2000; Maidment & Barrett, 2011). Though extant archosaurs can provide a basis for soft tissue reconstruction, they provide poor analogs for the functional morphology of burrowing.

Burrowing behavior does occur in extant archosaurs, such as in burrowing owls (Thomsen, 1971), Magellanic penguins (Stokes and Boersma, 1991), blue penguins (Waas, 1990), American alligators (Martin et al., 2012), and Chinese alligators (Cheng-kuan, 1957). However these taxa do not provide an appropriate analog because the forelimbs of birds are specialized for flying, whereas the forelimbs of crocodilians are specialized for their sprawling gait and semi-aquatic lifestyle (Kley and Kearney, 2007). Burrowing has only been suggested for Koreanosaurus, based on its similarities to *Oryctodromeus* and its three dimensional preservation (Huh et al., 2010) and *Drinker* based on undescribed specimens (Bakker, 1996). Non-burrowing digging has been hypothesized for other dinosaur groups including forelimb digging for food acquisition in theropods (Senter, 2005; Simpson et al., 2010) and hind limb digging for nest-building in sauropods (Fowler and Hall, 2010). Fowler and Hall (2010) used an analog outside of the EPB, turtles, to explain the morphology and digging method in sauropods. The absence

of adequate analogs for digging within Archosauria necessitates an analysis of vertebrate groups outside of the EPB to compare the morphological adaptations for burrowing.

Digging within mammals, and the osteological and myological specializations associated with digging have been well documented. Many different styles of digging using the teeth, head and forelimbs have been documented in mammals. Three different methods of digging with the forelimbs are common in mammals, including humeral rotation digging, hook-and-pull digging, and scratch-digging (Hildebrand, 1985). The forelimb of *Oryctodromeus* does not appear to allow for significant rotation of the humerus and lack other osteological adaptations for humeral rotation digging such as a cranial shift of the glenoid or shortened forelimbs (Chapter 3, this volume). Additionally the forelimb does not exhibit the adaptations necessary for hook-and-pull digging such as an enlarged medial epicondyle of the humerus (Chapter 3, this volume). The final method of digging, scratch-digging, is used by many mammals such as armadillos, gophers, and squirrels, and yields specialized morphological features such as an enlarged olecranon, flared medial epicondyle of the humerus (Hildebrand, 1985). Scratch-digging in turtles and amphibians involves lateral sweeping of the forelimbs, due to the range of motion constraints of their sprawling gait (Kley and Kearney, 2007). In mammals, however scratch-digging comprises rapid, alternating strokes of the forelimbs in the parasagittal plane. In mammals, the muscle adaptations for scratch-digging generally allow for stabilization of the shoulder, and greater strength in flexing the digits, wrist, and humerus, and in extending the elbow. The muscle groups primarily used in burrowing are the teres major, the deltoid, scapular head of the triceps, the dorsoepitrochlearis, and latissimus dorsi (Hildebrand, 1985). In general, the muscles used in digging attach

posteriorly on the scapula and relatively distally on the humerus or on the olecranon process of the ulna to provide a more powerful lever arm in digging. Though specific morphological adaptations for digging in mammals may not be appropriate to compare with dinosaur morphology, the biomechanical constraints for digging would likely be similar, as the forelimbs share a general homology.

The objectives of this study are twofold: (1) to generate a musculature reconstruction using the EPB, previous ornithischian muscle reconstructions, and osteological correlates present on specimens of *Oryctodromeus*, and (2) to use the musculature reconstruction to elucidate any possible advantages or adaptations for burrowing relative to the adaptations seen in mammals, as the EPB provides no analogs for specialized diggers.

MATERIALS AND METHODS

The forelimb musculature reconstruction of *Oryctodromeus* was generated based on the literature on the forelimb musculature of crocodilians, birds, and other ornithischian dinosaurs. The musculature of crocodilians (*Alligator mississippiensis* in Reese, 1915; and a generalization based on dissections of *Alligator mississippiensis*, *Crocodylus siamensis*, *Crocodylus acutus*, *Osteolaemus tetraspis* and *Gavialis gangeticus* in Meers, 2003) and birds (*Apteryx australis mantelli* or Brown Kiwi in McGowan, 1982; *Gallus gallus domesticus* in Yasuda, 2002) were used as representatives of the EPB. Reconstructions of the appendicular musculature of *Lesothosaurus* (Maidment and Barrett, 2011) and *Camptosaurus* (Carpenter and Wilson, 2008), and the appendicular and axial muscular reconstruction of *Maiasaura* (Dilkes, 2000) were also used as comparisons in this reconstruction. All three ornithischian reconstructions used the EPB

to analyze whether a muscle group was likely present in dinosaurs, though their methods varied.

In generating a muscle reconstruction, the first step is to determine whether or not a muscle group is present. Presence or absence, and the degree of certainty with which a muscle can be included in a reconstruction, is determined using the EPB. Witmer (1995) described a method of categorizing the confidence with which a soft tissue feature can be reconstructed within the EPB framework, describing the presence or absence of a soft tissue feature using levels of inference. The six levels of inference range from 1 to 3', and take into account presence or absence of a muscle group in the EPB, and the presence or absence of osteological correlates in the EPB (Table 4.1). Level 1 inference indicates that a muscle group is present in both groups of extant relatives, and that osteological correlates for that muscle group are present in both groups. Level 1' inference indicates that a muscle group is present in both groups of extant relatives, but osteological correlates for the muscle are not present in one or both taxa. Level 1 and 1' inferences suggest that outgroup analysis supports the presence of a particular feature. Level 2 inference indicates that a muscle is present in one group of extant relatives and exhibits osteological correlates. Level 2' inference indicates that a muscle group is present in one group of extant relatives, but osteological correlates are absent. Level 2 and 2' inferences suggest that a feature is equivocally present. Level 3 inference indicates a derived soft tissue characteristic that is absent in both groups of extant relatives, but is supported by other morphological evidence. Level 3' inference indicates a soft tissue characteristic that is absent in extant relatives and has little other morphological evidence to support it.

Level 3 and 3’ inferences suggest a high degree of uncertainty about the presence of a feature.

Therefore, a muscle group present in both birds and crocodilians would be supported by the EPB, and should be included in a reconstruction. A muscle group present in either birds or crocodilians would be equivocally present, as it is possible that the muscle group is an apomorphy of either the lineage of birds or of crocodilians. Whether or not a level 2 or 2' inference was reconstructed then relies on further morphological and phylogenetic evidence, described later. Muscle groups absent in both birds and crocodilians were excluded from the reconstruction.

When the EPB supported the presence of a muscle, a comparison of the origins and insertions of muscles in birds and in crocodilians was used to find the possible origin and insertion sites in dinosaurs. If attachment sites were found in homologous locations in birds and crocodilians, then the muscle likely had similar origin and insertion sites in dinosaurs. When origin and insertion sites differed between birds and crocodilians, further evidence was necessary to generate a more accurate reconstruction. Osteological correlates of muscle attachment sites, such as pitted or striated muscle scars, or the presence of tubercles or ridges, were used to aid in these cases.

The humeri, scapulae, and coracoids of adult specimens of *Oryctodromeus* (MOR 1636a and MOR1642) were analyzed for the presence osteological correlates, but as previous studies have suggested, the presence of osteological correlates do not necessarily provide an accurate estimate of the extent of an attachment site, and the absence of an osteological correlate does not necessarily indicate the absence of a particular muscle (McGowan, 1982; McGowan, 1986; Bryant and Seymour, 2005). When

the locations of the origins and insertions were consistent within the EPB, muscle scars could be associated with a muscle group with greater certainty. When there was inconsistency between origins and insertions in birds and crocodilians, the position of a muscle scar helped determine whether a muscle attachment site was more crocodilian-like or avian-like.

In cases where the EPB provided inconsistent origin and insertion sites, and specimens of *Oryctodromeus* exhibited no osteological correlates associated with a muscle, the studies of *Lesothosaurus* (Maidment and Barrett, 2011), *Maiasaura* (Dilkes, 2000), and *Camptosaurus* (Carpenter and Wilson, 2008) provided more resolution. In some cases, though *Oryctodromeus* lacked osteological correlates for a particular muscle, other ornithischian dinosaurs did present osteological correlates for that muscle. The presence of osteological correlates in other ornithopod taxa provided a potential location for the attachment site of the muscle in the reconstruction.

All three of these earlier studies resulted in similar musculature reconstructions, however their method of reconstruction varies slightly. Maidment and Barrett (2011) used only muscle groups with a level of inference of 1 or 1’ in their reconstruction. Dilkes (2000) reconstructed muscle groups with a 1 or 1’ level of inference, but also included muscle groups with a 2 or 2’ level of inference if non-archsaurian reptiles exhibited the feature or if osteological correlates were present on *Maiasaura* specimens (Dilkes, 2000), suggesting that one of the outgroups secondarily lost the trait (as in Bryant and Russell, 1992). Carpenter and Wilson (2008) included muscle groups with a level of inference of 2 and 2’ in their reconstruction. The reconstruction of *Oryctodromeus* includes the appendicular musculature which originates or inserts on the

scapula and humerus that are described in all three of the aforementioned reconstructions, and the axial musculature which inserts onto the scapula described for *Maiasaura* (Dilkes, 2000). The muscle groups included in the reconstruction were either inference levels of 1 or 1'; additional muscle groups with higher levels of inference (2 or 2') were only included if osteological correlates were present on specimens of *Oryctodromeus*. The locations of insertions and origins on the ulnae and radii were not reconstructed, because the *Oryctodromeus* material was too damaged to identify any osteological correlates.

RESULTS

Axial musculature included in the reconstruction are the levator scapulae, serratus superficialis, either the sternocoracoideus (present in birds) or costocoracoideus superficialis (present in crocodilians), and trapezius. The appendicular musculature reconstructed includes the biceps brachii, brachialis, coracobrachialis brevis, deltoideus clavicularis, deltoideus scapularis, latissimus dorsi, pectoralis, scapulohumeralis caudalis, subcoracoideus, subscapularis, supracoracoideus, triceps brevis, triceps longus, and teres major. Refer to Figure 4.2 for the muscle reconstruction of the scapula, and Figure 4.3 for the muscle reconstruction of the humerus.

Each muscle description includes the level of inference, the description of the location of the origin and insertion, as well as the number of heads (if applicable) in birds and crocodilians. The osteological correlates, if any, found on specimens of *Oryctodromeus* are detailed (Fig. 4.1), as well as the position of osteological correlates in *Maiasaura* and basal ornithischians (Dilkes, 2000; Maidment and Barrett, 2011). Finally the proposed position of the origin and insertion of the muscle is described (Table 4.2).

The descriptions of orientations in all of the different taxa are in reference to the life position of each taxon. Therefore, the scapulae of birds and dinosaurs are described with the long axis of the scapulocoracoid horizontal, with the glenoid facing ventrally. The scapulocoracoid of crocodilians are described with the long axis of the scapulocoracoid vertically, with the glenoid facing posteriorly. The humeri of birds and dinosaurs are described in a vertical orientation, whereas the humerus of crocodilians is described horizontally with the deltopectoral crest facing ventrally.

Axial Musculature

Levator scapulae (LSC) — The presence of the levator scapulae is equivocal in dinosaurs, as it is present in crocodiles but absent in birds, making it a level 2 or 2’ inference (Reese, 1915; Howell, 1937). In crocodiles, the levator scapulae originates on the anterior cervical ribs and inserts on the medial surface of the anterior margin of the scapula (Meers, 2003). Despite its absence in birds, muscle scarring on the dorsal margin of the scapula corresponding with the location of the insertion in crocodiles is present in specimens of *Oryctodromeus*. In *Oryctodromeus* the dorsal margin of the scapular blade exhibits two distinct sets of linear scars; the anterior set of scars form at a 30^{o} angle from the margin of the blade and extend half the length of the scapular blade, whereas the posterior scars are at a smaller angle, subparallel to the blade margin and extend the posterior half of the length of the blade. The position of the posterior set of scars is parsimonious with the insertion site of the levator scapulae, despite the equivocal presence in dinosaurs. The higher angle anterior scars likely correlate with the trapezius. Therefore, despite being a level 2 or 2' inference in *Oryctodromeus*, the levator scapulae

likely originated on the cervical ribs as in crocodilians and most other vertebrates, and inserted on the posterior half of the dorsal margin of the scapula.

Serratus superficialis (SES) – The presence of the serratus superficialis (or serratus ventralis thoracic in Meers, 2003) in both birds and crocodilians supports the presence of the serratus superficialis as a level 1 or 1' inference in dinosaurs, though it is uncertain whether the serratus superficialis has one or two divisions. The serratus superficialis in crocodilians has a single division, and inserts on the posterodorsal margin of the scapular blade (Meers, 2003). In birds, the serratus superficialis consists of two divisions (pars cranialis and pars caudalis), which have fleshy insertions on the posterior edge of the medial surface of the scapula (McGowan, 1982). In *Oryctodromeus* the entire ventral margin of the scapular blade has faint, uniform striations. As the ventral margin of the scapular blade is also the attachment site for the scapulohumeralis caudalis, it is impossible to differentiate the posterior margin of the attachment site of the scapulohumeralis caudalis and the anterior margin of the attachment site of the serratus superficialis. However the extent of scarring posteriorly on the ventral margin of the scapular blade, as well as the support of the EPB, indicates that the serratus superficialis was likely present in *Oryctodromeus,* inserting on the ventral margin of the scapular blade.

Sternocoracoideus and/or Costocoracoideus Superficialis (STC or CCS) – The sternocoracoideus and the costocoracoideus superficialis share similar origins and insertions in the EPB of dinosaurs, however, they are not homologous, as both are present in lepidosaurs (Abdala and Diogo, 2010). The former is present in birds (McGowan, 1982), the latter present in crocodiles (Reese, 1915; Meers, 2003). As the

sternocoracoideus is present in lepidosaurs and birds, it is considered a level 1 or 1' inference, whereas the costocoracoideus superficialis is a level 2 or 2' inference. The presence of one or both of these muscles is potentially supported by the EPB, though it is equivocal which muscle was present. The sternocoracoideus originates on the sternocoracoidal process of the sternum (McGowan, 1982), and the costocoracoideus superficialis originates on the first sternal rib (Meers, 2003). Both insert on the ventromedial surface of the coracoid (Meers, 2003; McGowan, 1982). No sternal material is known for *Oryctodromeus*, therefore the origins of both muscles are not reconstructed, and cannot aid in determining which muscles are present. However, a fossa on the ventral surface of the coracoid between the sternal process of the coracoid and the coracoidal glenoid buttress marks the potential insertion of the sternocoracoideus and/or the costocoracoideus superficialis. Scarring present on *Oryctodromeus* does not indicate whether one or two distinct muscle groups inserted at the site, therefore the osteological correlate may support the presence of both of the sternocoracoideus and the costocoracoideus superficialis, or just one of the muscle groups. The sternocoracoideus is a level 1 or 1’ inference, indicating it was likely present, but the costocoracoideus superficialis, being a level 2 or 2’ inference with a potential osteological correlate present in specimens of *Oryctodromeus* means it may also be present. The two muscles are grouped together in this reconstruction because based on the criteria used for reconstruction, it is impossible to separate the costocoracoideus superficialis from the sternocoracoideus given the known material for *Oryctodromeus.*

Trapezius (TRA) – The presence of the trapezius is equivocal in dinosaurs. It is absent in *Apteryx* (McGowan, 1982) and *Gallus* (Yasuda, 2002), but is present in

crocodilians (Reese, 1915; Meers, 2003), making it a level 2 or 2' inference. In crocodilians, the trapezius originates from the thoracodorsal fascia and inserts on the dorsal region of the anterior margin of the scapular blade (Meers, 2003). In *Oryctodromeus* the dorsal margin of the scapular blade exhibits a small tubercle just posterior to the acromion that may indicate the anterior margin of the trapezius, and a series of linear scars along the dorsal margin of the scapular blade which show the extent of the trapezius. The anterior scars angle posterodorsally at an angle of about 30^{o} from the dorsal margin of the scapula, and are parsimonious with the position of the insertion of the trapezius. The scars that form at a lower angle to the dorsal margin are likely associated with the levator scapulae. Despite the equivocal support from the EPB, the presence of osteological correlates indicates that the trapezius was likely present in *Oryctodromeus*, inserting on the anterior region of the dorsal margin of the scapular blade, and originating via a fascia on the midline.

Appendicular Musculature

Biceps brachii (BIC) – The presence of the biceps brachii is a level 1' inference, being present in both birds and crocodilians. In ratites, the biceps brachii has a single head originating on the coracoid, whereas in other birds there are two heads to the biceps brachii. It inserts via tendon on the proximal radius (McGowan, 1982). In crocodilians the biceps brachii originates via a wide, flat tendon from the anterodorsal edge of the coracoid, and inserts on the proximal radius (Meers, 2003). The origins and insertions of the biceps brachii in crocodilians and birds are roughly coincident. The biceps brachii likely originated on the lateral coracoid and inserted on the proximal radius in *Oryctodromeus*. However the surface of the coracoid of *Oryctodromeus* is flat and devoid

of osteological correlates that would indicate the origin of the biceps brachii, and the insertion site on the radius could not be identified. *Maiasaura* exhibits a tubercle on the anterodorsal margin of the coracoid marking the presence of the biceps brachii (Dilkes, 2000), but basal ornithischians do not exhibit any osteological correlates for the muscle (Maidment and Barrett, 2011). As the presence of the biceps brachii is a level 1' inference, its presence is strongly supported by the EPB. Though no osteological correlates occur in *Oryctodromeus,* the presence of osteological correlates in *Maiasaura* aid in determining the position of the origin of the biceps brachii, which would have been on the lateral surface of the coracoid anterodorsal to the coracoid foramen. It is unclear whether the biceps brachii had one or two heads in *Oryctodromeus.*

Brachialis (BRA) – The presence of the brachialis in dinosaurs is a level 1' inference. In birds the origin of the brachialis is fleshy and located on the anterior surface of the distal end of the humerus. It inserts on the proximal end of the ulna. Neither the insertion nor the origin produces an osteological correlate (McGowan, 1982). In crocodilians the brachialis originates on the anteroventral region of the humeral shaft, distal to the deltopectoral crest. It inserts on the posterior surface of the radius (Meers, 2003). The origin of the brachialis is consistent between crocodilians and birds, indicating that dinosaurs likely shared a similar origin. However no osteological correlates are present in specimens of *Oryctodromeus,* nor are osteological correlates present for the origin of the brachialis in *Maiasaura* or basal ornithischians (Dilkes, 2000; Maidment and Barrett, 2011). Based on the consensus for the position of the origin of the brachialis in birds and crocodilians, in *Oryctodromeus* the biceps brachii likely originates on the anteromedial surface of the distal half of the humerus, superior to the ulnar

condyle. The position of the insertion is more uncertain, as in birds the biceps brachii inserts on the ulna, and in crocodilians it inserts on the radius. As the radius and ulna were not included in the reconstruction, the insertion site is equivocal but is either on the posterior proximal ulna or radius.

Coracobrachialis brevis (CBB) – The presence of the coracobrachialis brevis in dinosaurs is a level 1' inference. The coracobrachialis has two heads within crocodilians, the ventralis and dorsalis, which originate broadly on the coracoid from the ventral margin to the coracoid foramen and on the lateral surface of the ventral scapula posterior to the origin of the deltoideus clavicularis, respectively. The ventralis and dorsalis heads of the coracobrachialis insert medial to the deltopectoral crest of the humerus and dorsolateral to the deltopectoral crest, respectively (Meers, 2003). In ratites the coracobrachialis has one head originating on the ventrolateral surface of the coracoid anterior to the glenoid and inserting on the anterior surface of the proximal humerus (McGowan, 1982). In *Oryctodromeus* the insertion of the coracobrachialis is marked by a series of vertical scars on the anterior surface of the humerus medial to the proximal deltopectoral crest, however there are no osteological correlates for the origin of the coracobrachialis. Based on the presence of osteological correlates as well as consistency within the EPB, the coracobrachialis in *Oryctodromeus* inserts on the anterolateral surface of the proximal humerus. Though there is no osteological correlate for origin of the coracobrachialis, its location on the ventrolateral surface of the coracoid is supported by the EPB analysis, though it is unclear whether it had one or two heads.

Deltoideus clavicularis (DCL) – The deltoideus clavicularis is supported by the EPB analysis as a level 1' inference. Romer (1944) homologized the deltoideus

clavicularis in crocodilians to the scapulohumeralis cranialis in birds. In crocodilians, the deltoideus clavicularis originates fleshily from acromion of the anterior scapula and inserts on the anterior humerus lateral to the deltopectoral crest (Meers, 2003). In *Apteryx* the scapulohumeralis cranialis is absent (McGowan, 1982), however in *Gallus* the scapulohumeralis cranialis originates on the clavicle and insert on the anterior surface of the proximal humerus (Yasuda, 2002). In *Oryctodromeus* no textural scarring is present on the scapula to indicate the origin of the deltoideus clavicularis, however in the reconstruction of basal ornithischians, the prominent acromion process is considered an osteological correlate for the deltoideus clavicularis (Maidment and Barrett, 2011), and the scapular spine is even more prominent in *Oryctodromeus* (Chapter 3, this volume). In *Oryctodromeus* the deltoideus clavicularis inserts on the lateral surface of the deltopectoral crest and humeral shaft. The posterior margin of the insertion site is marked by a vertical ridge on the posterolateral edge of the humerus, posterior to the deltopectoral crest. As the origin site differs between crocodilians and birds, the position of the origin is somewhat equivocal, though the presence of the prominent acromion and absence of a clavicle in *Oryctodromeus* indicates that the deltoideus clavicularis likely originated on the dorsal aspect of the acromion process of the scapula. The support of the EPB and osteological correlates indicates the deltoideus clavicularis in *Oryctodromeus* inserted on the lateral surface of the deltopectoral crest of the humerus, with the deltoideus scapularis.

Deltoideus scapularis (DSC) – The deltoideus scapularis is supported as a level 1’ inference, being present in both birds and crocodilians. In crocodilians, the deltoideus scapularis originates fleshily on the lateral surface of the scapular blade, and inserts via

tendon on the lateral edge of the humerus proximal to the deltopectoral crest (Meers, 2003). In *Apteryx,* the deltoideus scapularis is called the deltoideus major and has two heads, which originate on the lateral surface of the scapula close to the coracoid via aponeurosis and insert via aponeurosis on the caudal surface of the proximal humerus (McGowan, 1982). In *Oryctodromeus* no osteological correlates are present to indicate the origin of the deltoideus scapularis, but the insertion, with the insertion of the deltoideus clavicularis, is marked by the ridge on the posterolateral edge of the humerus. As in *Oryctodromeus,* no osteological correlates mark the origin of the deltoideus scapularis in *Maiasaura* or other basal ornithischians (Dilkes, 2000; Maidment and Barrett, 2011). Because the origin of the deltoideus scapularis is consistent between birds and crocodilians, originating broadly on the lateral surface of the scapular blade, the deltoideus scapularis can be inferred to originate similarly in *Oryctodromeus*. The insertion on the lateral aspect of the deltopectoral crest of the humerus with the deltoideus clavicularis is supported by osteological correlates.

Latissimus dorsi (LAT) – The latissimus dorsi is supported as a level 1 inference, due to the presence of osteological correlates in both birds and crocodilians. In crocodilians, the latissimus dorsi originates from the thoracodorsal fascia and inserts via tendon on the dorsal surface of the humerus on which there is a prominent tubercle or pit indicating the insertion (Meers, 2003). In most birds the latissimus dorsi is separated into two heads, the cranialis and caudalis, however in *Apteryx* only the caudalis is present. The latissimus dorsi originates via aponeurosis from the neural spine of last cervical and first several thoracic vertebrae and inserts via a tendon on the posterior surface of the humeral shaft (McGowan, 1982). Unlike in birds and crocodilians, no osteological

correlates for the origin and insertion of the latissimus dorsi are present in *Oryctodromeus.* In *Maiasaura* the presence of a tubercle on the posterior surface of the proximal humerus indicated the insertion of the latissimus dorsi, though osteological correlates are absent in some basal ornithischians (Dilkes, 2000; Maidment and Barrett, 2011). As in crocodilians and birds, in *Oryctodromeus* the latissimus dorsi likely originates on the lumbodorsal fascia and inserts on the posterior surface of the proximal humerus via a tendinous attachment shared with the teres major (if present).

Pectoralis (PEC) – The presence of the pectoralis is a level 1 inference, due to the presence of osteological correlates in both birds and crocodilians. In crocodilians, the pectoralis has two or three heads originating on the sternum and inserting fleshily on the apex of the deltopectoral crest of the humerus (Meers, 2003). In birds, the pectoralis is divided into four heads, however only one is present in ratites, except in *Apteryx*, which has two heads. The two heads of the pectoralis present in *Apteryx* are the pars thoracicus and the pars abdominalis, which originate from the coracoid and sternum, and from the abdominal region, respectively. The two heads insert by aponeurosis to the anterior surface of the proximal humeral shaft (McGowan, 1982). The presence of osteological correlates is unknown for the origin, as there is no sternal material preserved from *Oryctodromeus;* however the insertion is marked by a dorsoventrally expanded scarred surface on the apex of the deltopectoral crest. Similarly, in both *Maiasaura* and *Lesothosaurus*, the pectoralis originates on the sternum, though no osteological correlates are described, and inserts on the apex of the deltopectoral crest, with osteological correlates present marking the insertion (Dilkes, 2000; Maidment and Barrett, 2011). Based on the correspondence of the attachment sites in crocodilians and birds, it is likely

that in *Oryctodromeus* the pectoralis originates on the sternum (not reconstructed) and inserts on the apex of the deltopectoral crest of the humerus. The number of heads in dinosaurs is equivocal.

Scapulohumeralis caudalis (SHC) – The scapulohumeralis caudalis is a level 1' inference in dinosaurs. In crocodilians the scapulohumeralis caudalis originates from the ventral half of the posterior margin of the scapular blade and inserts broadly over the dorsal view of proximal humerus (Meers, 2003). In *Apteryx* the scapulohumeralis caudalis originates on the ventrolateral edge of the scapula and inserts via tendon on the posterior surface of the proximal humerus (McGowan, 1982). In *Oryctodromeus* a small tubercle and a series of faint lineations are present on the anteriormost ventral edge of the scapular blade marking the origin of the scapulohumeralis caudalis along with the serratus superficialis. Faint lineations on the posterior surface of the proximal humerus, lateral to the humeral head indicate the insertion. The position of these muscle scars coincide with the position of scarring present in *Maiasaura* and *Lesothosaurus* (Dilkes, 2000; Maidment and Barrett, 2011). The scapulohumeralis caudalis of *Oryctodromeus* originates on anterior half of the ventral edge of the scapular blade, between the triceps longus and serratus superficialis, and inserts on the posterior surface of the proximalmost humerus, lateral to the humeral head.

Subcoracoideus (SBC) – The subcoracoideus is present in birds, but absent in crocodilians. However its presence in lizards and other lepidosaurs (Romer, 1944) leads to the conclusion that the loss of the subcoracoideus is an apomorphy of extant crocodilians. Therefore, despite its absence in crocodilians, its presence in *Oryctodromeus* represents a level 1' inference (Maidment and Barrett, 2011). In *Apteryx*,

the subcoracoideus is small and originates from the medial surface of the scapulocoracoid, and inserts via aponeurosis to the proximal humerus (McGowan, 1982). In *Oryctodromeus,* there are no osteological correlates that would correspond with the origin of the subcoracoideus. However there is faint scarring on the margin of the medial tuberosity of the proximal humerus that corresponds with the location of the insertion site. There are no osteological correlates present for either *Lesothosaurus* or *Maiasaura* indicating either the origin or insertion site of the subcoracoideus (Maidment and Barrett, 2011; Dilkes, 2000). Therefore, despite an absence in crocodilians, the presence of the subcoracoideus in lepidosaurs indicates that it was the basal condition, and that the EPB still supports the presence of the subcoracoideus. The presence of muscle scarring for the insertion in other ornithischians, and agreement between the position of the origin in birds, lizards, and other ornithischian reconstructions indicates that in *Oryctodromeus,* the subcoracoideus originates broadly on the medial surface of the coracoid anterior to the coracoid foramen, and inserts on the medial tuberosity of the proximal humerus with the subscapularis.

Subscapularis (SBS) – The subscapularis is present in dinosaurs as a level 1 inference (Maidment and Barrett, 2011). The subscapularis in crocodilians originates on the medial surface of the scapular blade, and inserts on the medial surface of the proximal humerus (Meers, 2003). In most birds the subscapularis has two heads, however in ratites, only one is present or well developed. In *Apteryx,* the subscapularis originates on the medial surface of the scapulocoracoid and inserts via tendon on the proximalmost humerus (McGowan, 1982). In *Oryctodromeus,* faint scarring on the medial tuberosity of the proximal humerus represents the insertion of the subscapularis, together with the

scapulohumeralis caudalis. However no osteological correlates mark the origin. In *Maiasaura* a concave surface on the medial scapular blade indicates the origin of the subscapularis, and scarring on the proximal humerus medial to the humeral head indicates the insertion (Dilkes, 2000), and *Scutellosaurus*, a basal thyreophoran, exhibits striations on the medial scapular blade interpreted as the origin of the subscapularis (Maidment and Barrett, 2011). The similarity of the insertion site on the medial surface of the scapula in birds and crocodilians, as well as agreement with other ornithischian reconstructions, indicates that despite the lack of osteological correlates in *Oryctodromeus*, the subscapularis likely originated broadly over the medial surface of the scapular blade. The insertion site, which is supported by the EPB and presence osteological correlates, was likely on the anteromedial surface of the proximal humerus with the scapulohumeralis caudalis. It is equivocal whether the subscapularis of *Oryctodromeus* had one or two heads.

Supracoracoideus (SCC) – The supracoracoideus is supported in outgroup analysis as a level 1' inference. In crocodilians, the supracoracoideus has three heads, the longus, intermedius, and brevis. The longus head of the supracoracoideus originates from the anterior half of the medial scapulocoracoid suture and the intermedius head originates on the anterior region of the lateral scapulocoracoid suture. The brevis head of the supracoracoideus originates on the anterodorsal region of the coracoid ventral to the origin of the intermedius. All three heads insert on the apex of the deltopectoral crest of the humerus (Meers, 2003). In birds, the supracoracoideus is used as a flight muscle, abducting the humerus, though in ratites the supracoracoideus is reduced and lacks this function. In birds the muscle has one head originating fleshily on the lateral coracoid,

passes through the triosseal canal, and inserts via tendon to the anterior surface of the distal humerus (McGowan, 1982). In *Oryctodromeus* the origin lacks osteological correlates that can be associated with the supracoracoideus, such as the triosseal canal seen in birds. A small facet proximal to the muscle scar of the pectoralis muscle marks the insertion of the supracoracoideus. There is inconsistency in the position of the origin in the EPB as well as in ornithischian musculature reconstructions. In *Maiasaura* scarring on the lateral surface of the coracoid indicates that the supracoracoideus originates broadly over the length of the dorsal margin of the coracoid (Dilkes, 2000). In basal ornithischians, the supracoracoideus has a limited origin on the anteriormost portion of the scapulocoracoid suture as in crocodilians. Though no surficial scarring is recognized, a surface anterior to the acromion may indicate the position of the origin of the supracoracoideus in *Stormbergia* (Maidment and Barrett, 2011). Based on the support of the EPB and osteological correlates, the insertion of the supracoracoideus is located dorsal to the apex deltopectoral crest of the humerus. The origin of the supracoracoideus is less certain, but is likely on the lateral surface of the scapulocoracoid, existing anywhere from anterior to the scapular spine of the acromion process to the dorsal margin of the coracoid. The pronounced anteroventral surface of the scapular spine may be associated with the origin of the supracoracoideus, indicating a potentially large origin for the supracoracoideus, but the extent is uncertain. The outgroup analysis is equivocal as to how may heads the supracoracoideus had in *Oryctodromeus*.

Teres major (TMA) – The teres major is equivocally present in dinosaurs as a level 2 inference. In crocodilians, the teres major originates broadly on the posterodorsal region of the lateral surface of the scapular blade, and inserts with the latissimus dorsi as

a tendon on a tubercle on the proximodorsal surface of the humerus (when oriented horizontally as in the sprawling gait of crocodilians; Meers, 2003). The teres major is absent in birds (Howell, 1937). In *Oryctodromeus* there are no muscle scars or tubercles present for either the origin or insertion of the teres major. Because no osteological correlates are present in *Maiasaura*, the teres major was not included in the reconstruction by Dilkes (2000). However in their reconstruction of *Camptosaurus* Carpenter and Wilson (2008) did include the teres major, identifying it on the posteroventral margin of the lateral surface scapular blade. They defined it in this position due to the separation of the scapular blade into two discrete surfaces, separated by a slight ridge extending from the acromion and continuing along the length of the scapula. The teres major cannot be reconstructed due to its equivocal presence and lack of osteological correlates, nevertheless its inclusion in the reconstruction of *Camptosaurus* and its association with the posteroventral margin of the scapular blade warrants mention. The teres major is shown in the reconstructions as equivocal (Figs. 4.2, 4.3, and 4.4) and is addressed further in the discussion.

Triceps brevis (TRIB) – The triceps brevis is supported by the EPB analysis as a level 1' inference, as it is present in all extant archosaurs, but leaves no osteological correlates. In crocodilians the triceps brevis comprises three heads, (1) the caudalis, (2) intermedialis, and (3) cranialis, originating (1) distal to the medial tuberosity of the humerus, (2) broadly on the ventromedial surface of the shaft of the humerus, and (3) as a narrow partially fleshy and partially aponeurotic attachment on the lateral surface of the shaft distal to the deltopectoral crest, respectively. All three heads insert on the ulna (Meers, 2003). In ratites, the triceps brevis (or humerotriceps) has one head originating

over much of the length of the posterior surface of the humerus. It inserts together with the triceps longus on the proximal ulna (McGowan, 1982). No osteological correlates are present on the humerus of specimens of *Oryctodromeus* to indicate the location of the origin of the triceps longus. As in *Oryctodromeus,* the triceps brevis of neither *Maiasaura* nor *Lesothosaurus* exhibits osteological correlates (Dilkes 2000; Maidment and Barrett 2011). Consensus between the origin and insertion of the triceps brevis in crocodilians and birds indicates that in *Oryctodromeus*, the triceps brevis originated broadly on the posterior surface of the humerus. The insertion, as in both outgroups, is on the proximal ulna. Outgroup analysis is equivocal as to how many heads of the triceps brevis were present in *Oryctodromeus.*

Triceps longus (TRIL) – The presence of the triceps longus is supported by the EPB analysis as a level 1' inference, though it is unclear whether there are one or two heads in dinosaurs. In crocodilians the triceps longus has two heads, the lateralis and caudalis, which originate on the posterior surface of the scapula dorsal to the glenoid and via a bifurcated tendon on the posterior surface of the scapula and coracoid respectively. Both heads insert on the ulna (ulnar musculature not reconstructed here; Meers, 2003). In ratites, the triceps longus (also called the scapulotriceps) originates as an aponeurosis from the ventral surface of the scapula posterior to the glenoid, and it inserts together with the triceps brevis on the posterior surface of the proximal ulna (McGowan, 1982). In *Oryctodromeus*, a scarred surface on the posteroventral surface of the glenoid buttress of the scapula marks the origin of one head of the triceps longus. The triceps longus inserts on the ulna, which is not reconstructed. Outgroup analysis is equivocal as to whether there were one or two heads of the triceps longus.

DISCUSSION

Implications for digging

In the original description of *Oryctodromeus*, Varricchio et al. (2007) proposed that *Oryctodromeus* used its forelimbs to construct the burrow in which it was discovered. Based on the osteological specializations of *Oryctodromeus* and the osteological adaptations for scratch-digging in mammals, such as a robust humerus with pronounced deltopectoral crest and scapula with enlarged acromion process and strongly posteroventrally expanded scapular blade, *Oryctodromeus* likely utilized scratch digging to construct its burrows. According to Hildebrand (1985), the muscle groups primarily used in scratch-digging are the scapular head of the triceps, the dorsoepitrochlearis, the latissimus dorsi, teres major, and deltoid, which all aid in the extension of the forelimb. In *Oryctodromeus* osteological evidence supports the presence of the scapular head of the triceps (triceps longus), and the EPB strongly supports the presence of the latissimus dorsi, deltoideus scapularis, and deltoideus clavicularis. The presence of the teres major, being a level 2' inference in dinosaurs, is equivocal, but will be further discussed due to its association with the posteroventral scapular blade. The dorsoepitrochlearis is a muscle group only found in mammals and may derive from either the triceps brachii or latissimus dorsi (Diogo et al., 2009). Figure 4.3 shows a simplified muscle reconstruction to show the lengths, origins, and insertions of the various muscle groups in life position.

The triceps brachii act to extend the antebrachium. As a typical adaptation of digging, the triceps longus originates distal from the scapular glenoid to allow for a stronger muscle action (Hildebrand, 1985). However, in *Oryctodromeus* the triceps longus inserts just posteriorly to the glenoid buttress, reducing the size of the lever arm.

This would not provide the strength in extension of the antebrachium seen in other digging organisms, due to the decreased leverage of the smaller lever arm. The triceps longus inserts on the olecranon process of the ulna, which follows a trend of increasing size with increasing fossoriality. The index of fossorial ability (IFA) is a common metric of fossoriality, which is calculated as the percentage of the total ulnar length relative to the length of the olecranon process (Vizcaíno et al., 1999), where values for fossorial mammals range from 20% to 90%. The olecranon process of *Oryctodromeus* is not enlarged, producing an IFA of 14.04% in MOR 1636, and 7.77% in MOR 1642 (though the ulnae are in poor condition, and these values are approximations), within the range of non-fossorial mammals. However, the articular surfaces preserved within dinosaurs may not reflect the true shape of the articular surface in life. The EPB supports the presence of cartilaginous epiphyses that are not preserved during fossilization as a level 1' inference (Holliday et al., 2010), though there is no osteological evidence for an enlarged olecranon cartilage in *Oryctodromeus*. Therefore, it is possible that the ulna of *Oryctodromeus* had a cartilaginous epiphysis may have extended the length of the olecranon process to allow for stronger antebrachium extension by the triceps longus.

Like in basal ornithischians, the latissimus dorsi of *Oryctodromeus* does not produce an osteological correlate as it does in *Maiasaura* (Dilkes, 2000). However the EPB does support the insertion of the latissimus dorsi on the posterior surface of the humerus. In crocodilians, the latissimus dorsi acts as an extensor of the humerus, lifting the humerus during locomotion (Meers, 2003). However the orientation of the pectoral girdle in ornithischians differs from that of crocodilians due to their distinct differences in locomotor modes. Crocodilians orient their scapulae vertically, and the humerus extends

laterally to allow for a sprawling gait, whereas the scapulae of bipedal ornithischians would have been oriented subhorizontally, with the humerus extended ventrally. While still acting as an extensor of the humerus, the latissimus dorsi also drew the humerus posteriorly along the sagittal plane. This would have aided in producing the repeated anteroposterior motion in the sagittal plane used in scratch-digging.

The deltoideus scapularis, and potentially the teres major, have broad origins on the distal scapular blade, and would provide a strong mechanical advantage in the retraction of the humerus. However, the teres major is equivocally present in dinosaurs, as it is not present in birds (Howell, 1937). The deltoideus clavicularis originates dorsal to the pronounced scapular spine. The deltoideus scapularis, deltoideus clavicularis, and teres major are significant muscle groups used in digging, therefore the broadly expanded posterior blade of the scapula would have provided a large surface area for a broader attachment, larger muscle mass, and stronger muscle action. The teres major if present would insert with the latissimus dorsi on the posterior surface of the humerus, though no muscle scarring evidence shows how far distally the teres major and latissimus dorsi insert, therefore it is difficult to say how strong a lever arm would be produced by the teres major, if present. The deltoideus scapularis and deltoideus clavicularis insert on the lateral surface of the deltopectoral crest, which in *Oryctodromeus,* occupies roughly the proximal third of the humerus. The proximal insertion of the deltoideus scapularis would likely limit the strength of humeral retraction; however the insertion is positioned distally relative to the insertion in crocodilians, therefore providing a stronger muscle action than seen in crocodilians. In crocodilians, the deltoideus scapularis acts as a humeral abductor and stabilizer of the shoulder (Meers, 2003), however due to the difference in locomotor

style and pectoral girdle orientation, Maidment and Barrett (2011) suggested that the deltoideus scapularis may have retracted the humerus and provided some lateral rotation, and the deltoideus clavicularis may have abducted the humerus.

Limitations of the EPB

This musculature reconstruction of *Oryctodromeus*, based on the musculature of members of the EPB, is a morphologically conservative estimate of the presence and position of muscle groups. Similarly, the use of ratites as an avian representative may bias reconstructions more conservatively, due to the higher degree of uncertainty and variability in ratite forelimb myology. Because the forelimbs of ratites are vestigial, the musculature is not under a specific selection pressure, which results in higher variability in the presence, absence, and number of heads of muscle groups (Maxwell and Larsson, 2007), coupled with the often small sample sizes of myological descriptions, means that using ratites as an analog may insert more uncertainty into the reconstruction. Levels of inference (Witmer, 1995) are useful in determining the presence or absence of traits, but in the absence of osteological correlates on fossil material, the logistics of generating a reconstruction with accurate origin sites, insertion sites, attachment types, attachment extents is much more complicated. Though it would be tempting to generate biomechanical models of digging in *Oryctodromeus* based off of musculature reconstructions, the uncertainty associated with the position, size, and type of muscle attachment sites due to lack of osteological correlates makes these models nearly impossible to generate with any accuracy.

The EPB method is also limited in that apomorphies to ornithischians, ornithopods, and even *Oryctodromeus* specifically, are not considered, as they would be

level 3 or 3' inferences. This limitation is especially important to consider when analyzing the anterior scapula of *Oryctodromeus*, as it exhibits a pronounced morphological deviation from the morphology of extant analogs. The sharp scapular spine of the acromion process in *Oryctodromeus*, and to a lesser degree in *Orodromeus*, *Hypsilophodon*, and potentially *Zephyrosaurus*, presents a feature absent in birds and crocodilians. The presence of the scapular spine probably had a morphological significance, such as anchoring a large muscle groups on either side, similar to the infraspinatus muscle relative to the scapular spine of mammals. The deltoideus clavicularis originates dorsal to the scapular spine, and the supracoracoideus originates anterior to the dorsal margin of the scapular spine. However along most of the anteroventral margin of the scapular spine, there is no compelling evidence from the EPB supporting a particular muscle group in this location as neither birds nor crocodilians have such a prominent scapular spine or concavity ventral to the spine. In crocodilians, a second head of the coracobrachialis, the coracobrachialis brevis dorsalis, originates in a similar position, however it has no association with a spine (Meers, 2003), and birds do not possess this second head (McGowan, 1982). The coracobrachialis protracts and adducts the humerus, which would potentially act as an antagonistic muscle group to the deltoideus scapularis, teres major, and latissimus dorsi (Maidment and Barrett, 2011), important muscles in the digging stroke. It is unclear what muscle group inhabits this region ventral to the scapular spine, however, whether it is a broader origin of the supracoracoideus, a second head of the coracobrachialis as seen in crocodilians, or a muscle group present as an apomorphy of ornithopods. No other significant

morphological features remain unexplained or as equivocal in the proposed musculature reconstruction.

Despite lack of support from the EPB for many axial muscle groups, the axial musculature of the *Oryctodromeus* leave several prominent muscle scars along the margins of the scapula. As in *Maiasaura* (Dilkes, 2000), the levator scapulae, trapezius, and serratus superficialis all produce scarring on the lateral surface of the scapular blade. These muscles all act to protract and stabilize the pectoral girdle. Strong insertions for the axial musculature would provide stability for the forelimb and pectoral girdle while performing powerful digging strokes. Unfortunately, the musculature reconstruction of basal ornithischians did not include the axial musculature, so the abundance of axial muscle scars in *Oryctodromeus* relative to basal ornithischians and basal ornithopods remains unclear. The abundance of axial muscle scars in *Maiasaura* may be due to the necessity for stabilization of the pectoral girdle necessary for quadrupedal locomotion.

The lack of osteological correlates and differences between the musculature of crocodilians and birds limit the amount of recoverable detail in the forelimb musculature reconstruction of *Oryctodromeus.* However, the details obtainable via the EPB and osteological correlates allow an approximation of soft tissue anatomy of *Oryctodromeus* and its functional significance. The presence of an enlarged deltoideus scapularis and equivocally the teres major, corresponding with a ventrally expanded scapular blade, indicate a strong retraction of the humerus, where a strong coracobrachialis brevis, which may potentially have had two heads, would have allowed for protraction of the humerus. The triceps brachii acted to extend the elbow, which likely had a large range of motion. However the location of the triceps longus, as well as a relatively small olecranon

process, may have limited the strength of this muscle action. These slightly specialized features provide evidence of adaptation for burrowing in *Oryctodromeus.*

CONCLUSION

The forelimb of *Oryctodromeus* exhibits osteological specializations beneficial for digging relative to other basal ornithopods, including an expanded acromion with sharp scapular spine, a broadly expanded posteroventral margin of the scapular blade, and a more robust humerus with strongly anteriorly projecting deltopectoral crest. These osteological features can be correlated with the musculature used in digging in mammals, especially the deltoideus clavicularis, deltoideus scapularis, and potentially the teres major. The posterior scapular blade of *Oryctodromeus* has a much larger surface area relative to the overall size of the scapula when compared to other ornithischian and ornithopod reconstructions (Dilkes, 2000; Maidment and Barrett, 2011), potentially allowing for relatively larger muscle attachment sites.

Of the muscle groups important for digging in mammals, the triceps longus, deltoideus scapularis, and latissimus dorsi are present, the teres major is equivocally present, and the dorsoepitrochlearis is absent in dinosaurs. The positions of the origin and insertion of the triceps longus do not appear strongly adapted for the requirements for digging, as it would provide a weak lever arm. The broad insertions of the deltoideus scapularis and potentially the teres major over the posteroventral scapular blade support the necessity for a strong muscle action in digging, and the insertions on the proximal half of the humerus would have generated a moderate lever arm in retracting the humerus. Additionally, the relative abundance of muscle scarring on the scapula indicates axial musculature acted to stabilize the girdle against strong forces, such as powerful

digging strokes. Overall, the muscular adaptations for digging in the forelimb of *Oryctodromeus* are present but not extensive. The evidence for slight specialization for digging further supports the hypothesis that *Oryctodromeus* exhibited adaptations for constructing burrows. Many burrowing and denning vertebrates do not possess structural adaptations for digging, such as burrowing crocodilians primarily adapted for semi-aquatic locomotion, and many denning mammals, e.g. rabbits, coyotes, and some rodents such as marmots and prairie dogs (Hildebrand, 1985; Kley and Kearney, 2007). As morphological adaptations for burrowing seem relatively conservative within mammals, the presence of any morphological features beneficial for digging supports that *Oryctodromeus* constructed the burrow in which it was discovered.

These features, though not conclusive evidence for fossoriality in *Oryctodromeus*, support the hypothesis. However, this study is limited by both the constraints of the homologies within the EPB, as well as the lack of an adequate analog within the EPB. Study in the morphological adaptations of burrowing reptiles may further elucidate adaptations for burrowing in non-mammalian groups, aiding in the interpretation of dinosaurian musculature. Furthermore, histological analysis of the forelimbs of *Oryctodromeus* could also provide better evidence of muscle attachment sites and regions of higher stress.

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TABLES

Table 4.1. The levels of inference for determining the presence or absence of a soft tissue feature, as described by Witmer (1995) with respect to dinosaur soft-tissue reconstructions. The use of lepidosaurs as an additional bracket, to determine whether a feature was secondarily lost was used in reconstructions by Maidment & Barrett (2011) and Dilkes (2000), though it was not defined in the original usage of the levels of inference by Witmer (1995).

Level of Inference	Description	Degree of Certainty
1	Soft tissue feature and an associated osteological correlate are present in both crocodilians* and birds.	Likely Present
1'	Soft tissue feature is present in both crocodilians* in birds, but osteological correlates are absent in one or both groups.	Likely Present
2	Soft tissue feature and an associated osteological correlate are present in either crocodilians* or birds.	Equivocal
2'	Soft tissue feature is present in either crocodilians* or birds, but no osteological correlates are present.	Equivocal
3	Soft tissue feature is absent from both crocodilians and birds, but other evidence suggests the presence of the feature.	Likely Absent
3'	Soft tissue feature is absent from both crocodilians and birds, and no evidence suggests the presence of the feature.	Likely Absent

*If a soft-tissue feature is absent in crocodilians, but present in both lepidosaurs and birds, it is likely that the basal condition was presence of the feature that was secondarily lost in crocodilians. Therefore, presence of the feature would remain a level 1 or 1' inference.

Table 4.2. Summary of the musculature reconstruction of *Oryctodromeus*. Osteological correlates refers to the presence of a scar feature at either the insertion or the origin, and is not specified in the table. For further detail, see the specific muscle description. Table modified from Maidment & Barrett 2011. Axial muscle group information from Dilkes, 2000 and Dilkes, 1993. Appendicular muscle group information from Maidment & Barrett, 2011.

	Muscle Group	Abbr.	Origin	Insertion	Level of Inference	OC present in *Oryctodromeus*	OC present in Maiasaura	OC Present in basal ornithischians
Axial	Levator scapulae	LSC	Cranial cervical ribs or transverse process of cervical vertebrae.	Dorsal margin of scapular blade	2 or 2’	Yes	Yes	N/A
	Serratus superficialis	SES	Last cervical rib and first few thoracic ribs.	Ventral margin of scapular blade	1 or 1’	Yes	Yes	N/A
	Sternocoracoideus and/or Costocoracoideus superficialis	STC or CCS	First sternal rib (CSC in crocodiles), Sternum (STC in birds)	(Both) Ventral surface posterior to sternal process.	1 or 1' (STC) 2 or 2’ (CCS)	Yes	Yes	N/A
	Trapezius	TRA	Thoracodorsal fascia	Dorsal margin of scapular blade	2 or 2’	Yes	Yes	N/A
Appendicular	Biceps brachii	BIC	Dorsolateral surface of coracoid	Proximal ulna or radius	1'	No	Yes	No
	Brachialis	BRA	Cranial surface of distal humerus	Proximal ulna and radius	1'	No	No	No
	Coracobrachialis brevis	CBB	Ventrolateral surface of coracoid	Medial surface of deltopectoral crest and cranial humerus	1'	No	Yes	Yes
	Deltoideus clavicularis	DCL	Acromial process of scapula	Lateral surface of deltopectoral crest of humerus	1'	Yes	Yes	Yes
	Deltoideus scapularis	DSC	Lateral surface of scapular blade	Lateral surface of deltopectoral crest of humerus	1'	Yes	Yes	Yes
	Latissimus dorsi	LAT	Last cervical and dorsal neural spines and thoracodorsal fascia	Caudal surface of humerus	1	No	Yes	No
	Pectoralis	PEC	Sternum	Apex of deltopectoral crest of humerus	1	Yes	Yes	Yes
	Scapulohumeralis caudalis	SHC	Ventral surface of scapular blade	Proximal humerus, lateral to humeral head	1'	Yes	Yes	Yes
	Subcoracoideus	SBC	Medial surface of coracoid	Medial tuberosity of humerus	1	Yes	No	No
	Subscapularis	SBS	Medial Surface of scapula	Medial tuberosity of humerus	1	Yes	Yes	Yes
	Supracoracoideus	SCC	Dorsal acromial process and scapulocoracoid suture	Apex of deltopectoral crest of humerus	1'	No	Yes	Yes
	Teres major	TMA	lateral surface of scapular blade	Caudal surface of humerus	2	No	No?	No
	Triceps brevis	TRIB	Caudolateral humerus	Olecranon process of ulna	1'	No	No	Yes
	Triceps longus	TRIL	Ventral surface of scapula close to glenoid	Olecranon process of ulna	1'	Yes	Yes	Yes

FIGURES

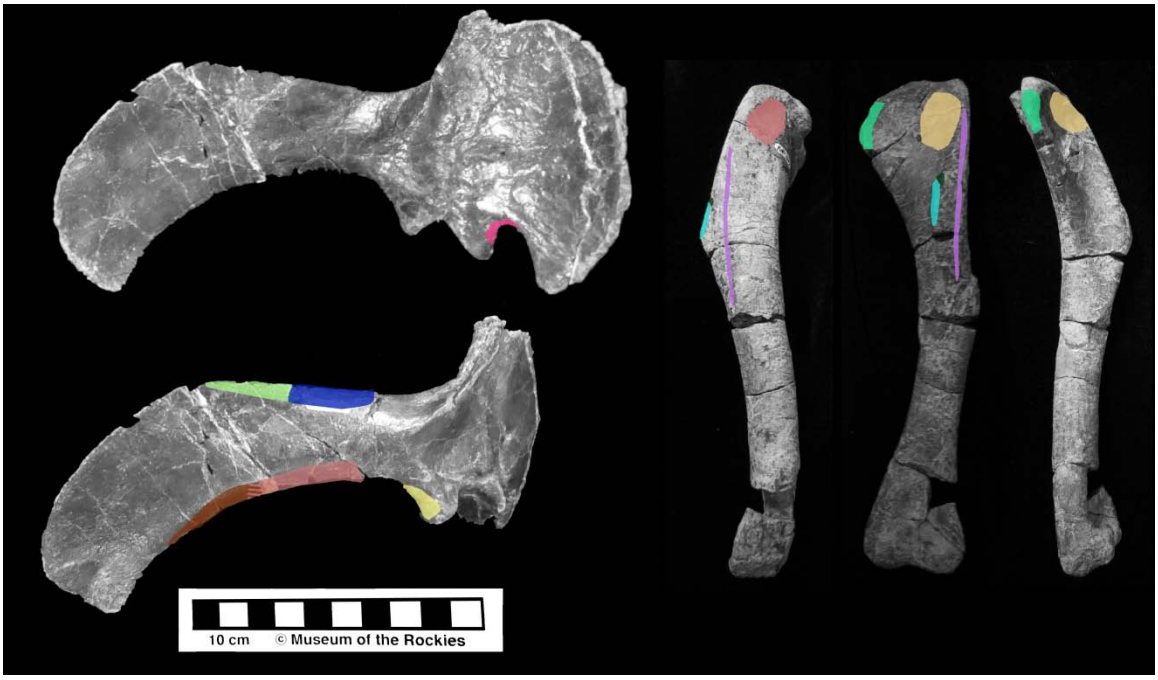

Figure 4.1. The locations of osteological correlates present on specimens of Oryctodromeus. The colors of the scarring sites correlate with the colors in the reconstructions on Figures 4.2 and 4.3.

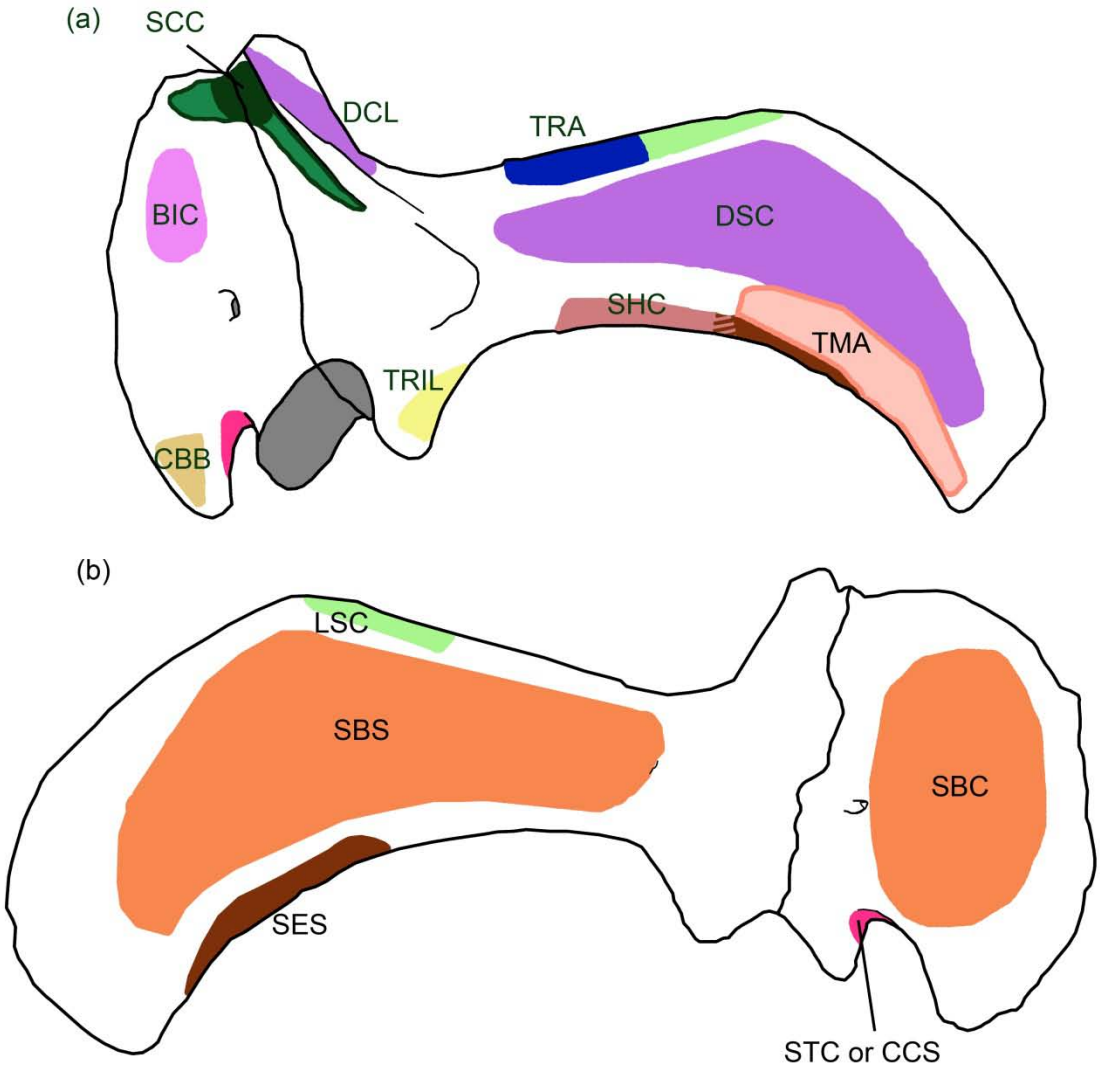

Figure 4.2. Muscle reconstruction of the scapulocoracoid of *Oryctodromeus cubicularis* in (a) lateral view and (b) medial view. Abbreviations explained in Table 1. The muscle groups which insert on the scapulocoracoid are the LSC, SES, TRA, and the STC or CCS. The muscle groups which originate on the scapulocoracoid are the BIC, CBB, DCL, DSC, SBC, SBS, SCC, SHC, and TRIL. Colors which are repeated in Figure 4.2 indicate origins. Attachment sites marked by a light color outlined in darker color (SCC and TMA) indicate equivocal muscle groups or positions not fully supported by EPB.

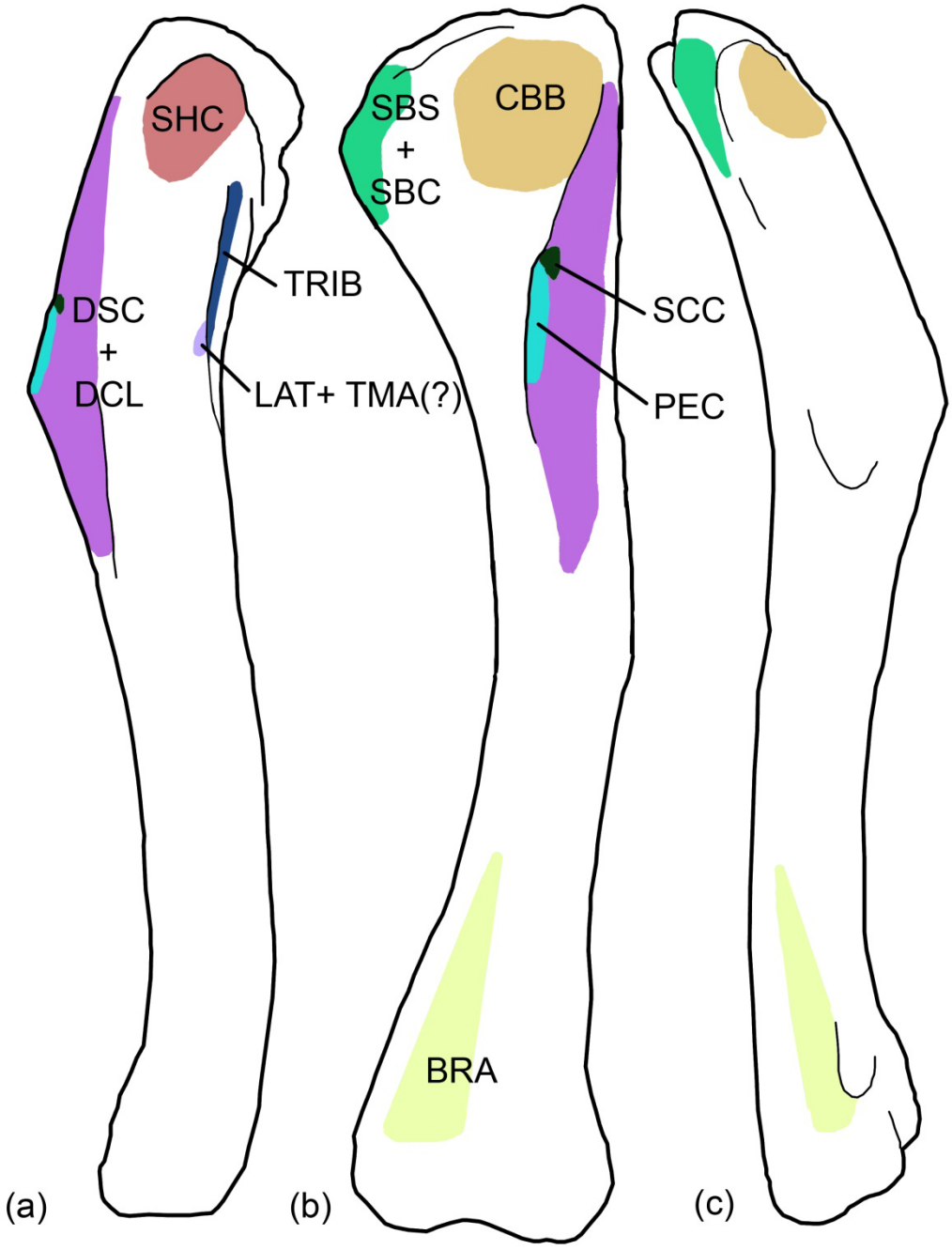

Figure 4.3 Muscle reconstruction of the humerus of *Oryctodromeus cubicularis* in (a) lateral view, (b) anterior view, (c) medial view. The muscle groups which insert on the humerus are the CBB, DCL, DSC, LAT, PEC, SBC, SBS, SCC, SHC, and TMA. The muscle groups which originate on the humerus are the BRA and TRIB. Abbreviations explained in Table 1. Colors repeated from Figure 4.1 indicate the insertion of the correlated muscle group in Figure 4.1.

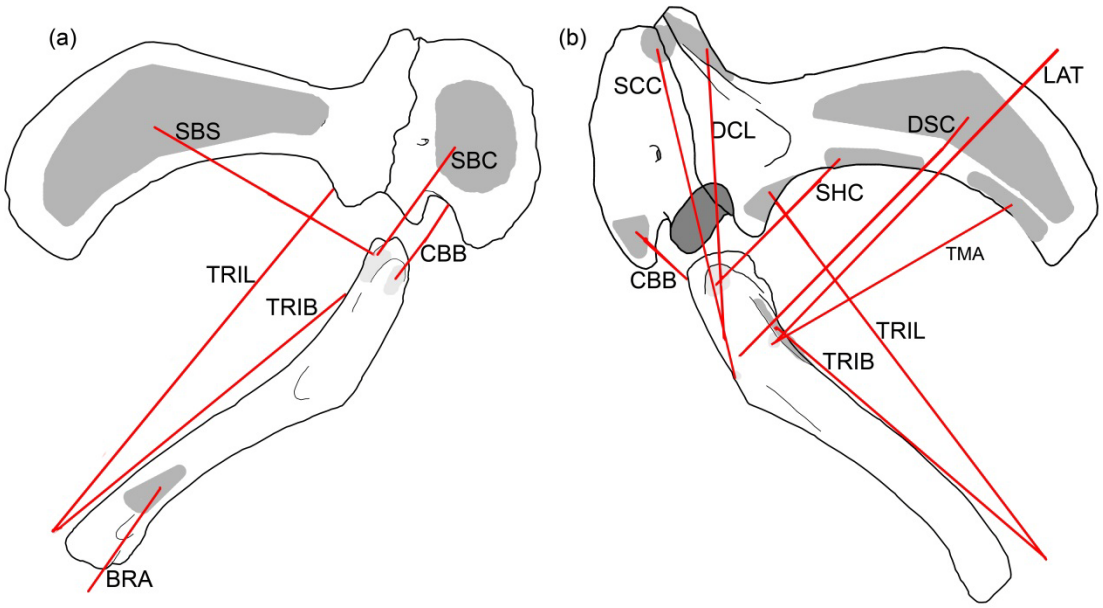

Figure 4.4. Simplified musculature diagrams of the shoulder complex of *Oryctodromeus cubicularis* in (a) medial view and (b) lateral view. The presence of the TMA is equivocal. Abbreviations for muscle groups are given in Table 4.2.

REFERENCES

Abdala, V., and R. Diogo. 2010. Comparative anatomy, homologies and evolution of the pectoral and forelimb musculature of tetrapods with special attention to extant limbed amphibians and reptiles. Journal of Anatomy 217:536–573.

Bakker, R. T. 1996. The real Jurassic park: dinosaurs and habitats at Como Bluff, Wyoming. The Continental Jurassic: Museum of Northern Arizona Bulletin 60:35–49.

Bryant, H. N., and A. P. Russell. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 337:405–418.

Bryant, H. N., and K. L. Seymour. 2005. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. Journal of Morphology 206:109–117.

Carpenter, K., and Y. Wilson. 2008. A new species of *Camptosaurus* (Ornithopoda: Dinosauria) from the Morrison Formation (Upper Jurassic) of Dinosaur National Monument, Utah, and a biomechanical analysis of its forelimb. Annals of Carnegie Museum 76:227–263.

Cheng-kuan, C. 1957. Observations on the life history of Chinese alligator (*Alligator sinensis* fauvel). Acta Zoologica Sinica 2:004.

Dilkes, D. W. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. Transactions-royal Society of Edinburgh 90:87–125.

Diogo, R., V. Abdala, M. A. Aziz, N. Lonergan, and B. A. Wood. 2009. From fish to modern humans – comparative anatomy, homologies and evolution of the pectoral and forelimb musculature. Journal of Anatomy 214:694–716.

Fowler, D. W., and L. E. Hall. 2010. Scratch-digging sauropods, revisited. Historical Biology 23:27–40.

Gilmore, C.W. 1915. Osteology of *Thescelosaurus*, an orthopodous dinosaur from the Lance Formation of Wyoming. Proceedings of the United Stations National Museum 49: 591-616.

Hildebrand, M. 1985. Digging of quadrupeds. Functional Vertebrate Morphology 89–109.

Holliday, C. M., R. C. Ridgely, J. C. Sedlmayr, and L. M. Witmer. 2010. Cartilaginous epiphyses in extant archosaurs and their implications for reconstructing limb function in dinosaurs. PLoS One 5:e13120.

Howell, A. B. 1937. Morphogenesis of the shoulder architecture: Aves. The Auk 54:364–375.

Huh, M., D. G. Lee, J. K. Kim, J. D. Lim, and P. Godefroit. 2010. A new basal ornithopod dinosaur from the Upper Cretaceous of South Korea. Neues Jahrbuch für Geologie und Paläontologie 259:1–24.

Kley, N. J., and M. Kearney. 2007. Adaptations for Digging and Burrowing; in Fins into limbs: evolution, development, and transformation. University of Chicago Press, pp. 284–309.

Maidment, S. C. R., and P. M. Barrett. 2011. The locomotor musculature of basal ornithischian dinosaurs. Journal of Vertebrate Paleontology 31:1265–1291.

Makovicky, P. J., B. M. Kilbourne, R. W. Sadleir, and M. A. Norell. 2011. A new basal ornithopod (Dinosauria, Ornithischia) from the Late Cretaceous of Mongolia. Journal of Vertebrate Paleontology 31:626–640.

Martin, A.J., M. Page, R.K. Vance, and S. Skaggs. 2012. Dens of the American alligator (*Alligator mississippiensis*) as traces and their predictive value for finding large archosaur burrows in the geologic record. Society of Vertebrate Paleontology: Program and Abstracts, 136.

Maxwell, E. E., and H. C. Larsson. 2007. Osteology and myology of the wing of the Emu (*Dromaius novaehollandiae*), and its bearing on the evolution of vestigial structures. Journal of Morphology 268:423–441.

McGowan, C. 1982. The wing musculature of the Brown Kiwi *Apteryx australis* mantelli and its bearing on ratite affinities. Journal of Zoology 197:173–219.

McGowan, C. 1986. The wing musculature of the Weka (*Gallirallus australis*), a flightless rail endemic to New Zealand. Journal of Zoology 210:305–346.

Meers, M. B. 2003. Crocodylian forelimb musculature and its relevance to Archosauria. The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology 274:891–916.

Nicholls, E. L., and A. P. Russell. 1985. Structure and function of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae). Palaeontology 28:643–677.

Parks, W. A. 1926. *Thescelosaurus warreni*, a new species of orthopodous dinosaur from the Edmonton Formation of Alberta. University of Toronto Studies Geology Series 21: 1-42.

Reese, A. M. 1915. The Alligator and Its Allies. GP Putnam's Sons.

Romer, A. S. 1944. The development of tetrapod limb musculature—the shoulder region of Lacerta. Journal of Morphology 74:1–41.

Scheetz, R. D. 1999. Osteology of *Orodromeus makelai* and the phylogeny of basal ornithopod dinosaurs. Montana State University–Bozeman.

Senter, P. 2005. Function in the stunted forelimbs of Mononykus olecranus (Theropoda), a dinosaurian anteater. Paleobiology 31:373.

Simpson, E. L., H. L. Hilbert-Wolf, M. C. Wizevich, S. E. Tindall, B. R. Fasinski, L. P. Storm, and M. D. Needle. 2010. Predatory digging behavior by dinosaurs. Geology 38:699.

Stokes, D. L., and P. D. Boersma. 1991. Effects of substrate on the distribution of Magellanic Penguin (*Spheniscus magellanicus*) burrows. The Auk 923–933.

Thomsen, L. 1971. Behavior and ecology of burrowing owls on the Oakland Municipal Airport. The Condor 73:177–192.

Varricchio, D. J., A. J. Martin, and Y. Katsura. 2007. First trace and body fossil evidence of a burrowing, denning dinosaur. Proceedings of the Royal Society B: Biological Sciences 274:1361–1368.

Vizcaíno, S. F., R. A. Fariña, and G. V. Mazzetta. 1999. Ulnar dimensions and fossoriality in armadillos. Acta Theriologica 44:309–320.

Waas, J. R. 1990. An analysis of communication during the aggressive interactions of little blue penguins (*Eudyptula minor*). Penguin Biology 345–373.

Witmer, L. M., and J. J. Thomason. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. Functional Morphology in Vertebrate Paleontology 1:19–33.

Yasuda, M. 2002. The Anatomical Atlas of *Gallus*. University of Tokyo Press, pp. 155-240.

CONCLUSION

The culmination of several studies on the basal ornithopod *Oryctodromeus cubicularis* indicates that there is strong support that *Oryctodromeus cubicularis* constructed burrows using scratch-digging with its forelimbs (Varricchio et al., 2007; Woodruff and Varricchio, 2011; Chapters 3 and 4, this volume). The discovery of specimens of *Oryctodromeus* within a distinct burrow structure initiated burrowing hypothesis (Varricchio et al., 2007), and actualistic experiments indicated that the level of disarticulation seen in the holotype specimens are possible for skeletons already present in a burrow (Woodruff and Varricchio, 2011). The morphometric analysis and musculature reconstruction of this study lend more support to the hypothesis that *Oryctodromeus* constructed, rather than stole, the burrow in which it was discovered.

The morphometric analyses indicated that though the morphology of the coracoid of *Oryctodromeus* does not have a functional significance for digging, the humerus does bear slight specializations beneficial for digging, and the scapula exhibits relatively strong specializations for digging. The humerus specimens of *Oryctodromeus* tend to be slightly more robust than other basal ornithopods, and have slightly longer deltopectoral crests than other basal ornithopods, though the specimens of *Oryctodromeus* do not appear to exceed the upper bounds of the range of variation seen in other basal ornithopods. A larger deltopectoral crest and more robust humerus would allow stronger strokes during digging. The scapula of *Oryctodromeus* exhibits specializations consistent with burrowing. The strong posteroventral expansion of the scapular blade increases the

surface area for muscle attachment, and the tall acromion process also provides a larger surface area for appendicular musculature.

The musculature reconstruction of *Oryctodromeus* indicated that the osteological specializations seen in *Oryctodromeus* do correspond with muscle groups advantageous for digging in mammals. The only major muscle used for digging in mammals equivocal in *Oryctodromeus* is the teres major, due to its absence in birds. Other muscle groups, such as the triceps longus, latissimus dorsi, deltoideus scapularis, and deltoideus clavicularis are present in *Oryctodromeus.* The triceps longus originates posterior to the scapular glenoid, likely too near the joint to provide significant mechanical advantage in retracting the humerus and extending the antebrachium. The latissimus dorsi acts as a retractor of the humerus. However the lack of osteological correlates on the humeri for the insertion makes it difficult to estimate how distal the insertion was located, therefore making it difficult to tell how powerfully the latissimus dorsi acted as a humeral retractor. The strongly expanded posteroventral margin of the scapular blade would have provided a large surface area for the origin of the deltoideus scapularis and the teres major, if present. However, no surficial scarring indicates the number or extent of muscle groups present on the posterior scapular blade, therefore the shape of the scapular blade alone cannot be attributed as an osteological correlate. The enlarged deltopectoral crest provides an enlarged surface area for the insertion of the deltoideus scapularis and deltoideus clavicularis. The enlarged acromion process provides an increased surface area for the origin of the deltoideus clavicularis. These features show inconclusive support for morphological adaptation for digging in *Oryctodromeus.* However when this evidence is coupled with other evidence supporting digging in *Oryctodromeus,* as well as the fact that

many organisms habitually construct dens and burrows without exhibiting morphological adaptations, the slight specializations seen in *Oryctodromeus* support the hypothesis of scratch-digging.

Both studies were limited by the fact that *Oryctodromeus*, as with all non-avian dinosaurs, are extinct. Soft-tissue preservation in the fossil record is rare, and musculature has never been well defined even in cases of exceptional preservation. Therefore studies of dinosaur soft-tissue morphology must use modern analogs, such as using the EPB to generate a musculature reconstruction, or using mammals as functional analogs to understand the specializations for digging because the EPB did not provide adequate functional analogs. However, using the EPB provides a conservative estimate of soft-tissue morphology, because it cannot account for muscles or divisions of muscles that evolved within extinct taxa, nor can it show if a muscle was lost in extinct taxa. It may also exclude muscle groups lost along either lineage of the EPB that do not present osteological correlates in fossilized material. Similarly, the lack of specialized burrowers within the EPB obscures understanding of the potential specializations for burrowing within archosaurs, which would serve as a closer analog. Instead it must be assumed that the adaptations for digging in archosaurs resemble the adaptations for digging in mammals. Finally, the common use of ratites as the avian representative of the EPB may potentially be misleading, as the forelimbs of ratites are vestigial, and have a high degree of variability (Maxwell and Larsson, 2007). Nevertheless, the EPB provides a rough estimate of the forelimb musculature and specializations for digging in *Oryctodromeus* and provides a solid foundation for further study of biomechanics and functional morphology within ornithopods.

Though digging has only recently begun to be explored in dinosaurs, already several different taxa within different groups of dinosaurs have been hypothesized as digging and burrowing, including marginocephalians such as *Protoceratops* (Senter, 2007; Longrich, 2010), theropods (Senter, 2005; Sereno, 2010; Simpson et al., 2010), sauropods (Fowler and Hall, 2010) as well as other basal ornithopods (Martin, 2009; Huh et al., 2010). However, the most compelling case for digging in dinosaurs remains *Oryctodromeus*, which was discovered in a burrow and exhibits osteological features consistent with those seen in mammals, and correspond to increases in the area of attachment sites of muscle groups used in digging. Further study into the histology or biomechanics of *Oryctodromeus* and further study of *Orodromeus* and *Zephyrosaurus*, those dinosaurs most closely related to *Oryctodromeus*, may further elucidate the role of digging in *Oryctodromeus*, and potentially other ornithopods.

REFERENCES CITED

Abdala, V., and R. Diogo. 2010. Comparative anatomy, homologies and evolution of the pectoral and forelimb musculature of tetrapods with special attention to extant limbed amphibians and reptiles. Journal of Anatomy 217:536–573.

Bakker, R. T. 1996. The real Jurassic park: dinosaurs and habitats at Como Bluff, Wyoming. The Continental Jurassic: Museum of Northern Arizona Bulletin 60:35–49.

Boyd, C. A., C. M. Brown, R. D. Scheetz, and J. A. Clarke. 2009. Taxonomic revision of the basal neornithischian taxa *Thescelosaurus* and *Bugenasaura*. Journal of Vertebrate Paleontology 29:758–770.

Boyd, Clint. 2012. Addressing the "Hypsilophodontid" problem in analyses of basal ornithischian relationships: new taxa, new data, new hypothesis. Society of Vertebrate Paleontology: Program and Abstracts: 67.

Bramble, D. M. 1982. Scaptochelys: generic revision and evolution of gopher tortoises. Copeia 852–867.

Bryant, H. N., and A. P. Russell. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 337:405–418.

Bryant, H. N., and K. L. Seymour. 2005. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. Journal of Morphology 206:109–117.

Butler, R. J., P. Upchurch, and D. B. Norman. 2008. The phylogeny of the ornithischian dinosaurs. Journal of Systematic Palaeontology 6:1–40.

Carpenter, K., and Y. Wilson. 2008. A new species of Camptosaurus (Ornithopoda: Dinosauria) from the Morrison Formation (Upper Jurassic) of Dinosaur National Monument, Utah, and a biomechanical analysis of its forelimb. Annals of Carnegie Museum 76:227–263.

Chapman, R., and M. Brett-Surman. 1990. Morphometric observations on hadrosaurid ornithopods; pp. 163–177 in Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, pp. 163-178.

Cheng-kuan, C. 1957. Observations on the life history of Chinese alligator (*alligator sinensis fauvel*). Acta Zoologica Sinica 2:004.

Dilkes, D. W. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. Transactions-Royal Society of Edinburgh 90:87–125.

Diogo, R., V. Abdala, M. A. Aziz, N. Lonergan, and B. A. Wood. 2009. From fish to modern humans – comparative anatomy, homologies and evolution of the pectoral and forelimb musculature. Journal of Anatomy 214:694–716.

Elissamburu, A., and S. F. Vizcaíno. 2004. Limb proportions and adaptations in caviomorph rodents (Rodentia: Caviomorpha). Journal of Zoology 262:145–159.

Fastovsky, D. E., and D. B. Weishampel. 2005. Ornithopods. The Evolution and Extinction of the Dinosaurs, 2nd ed. Cambridge University Press, pp. 186-218.

Fowler, D. W., and L. E. Hall. 2010. Scratch-digging sauropods, revisited. Historical Biology 23:27–40.

Galton, P. M. 1974. The Ornithischian Dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. British Museum (Natural History).

Galton, P. M. and J.A. Jenson. 1973. Skeleton of a Hypsilophodontid Dinosaur (Nanosaurus (?) rex) from the Upper Jurassic of Utah. Brigham Young University Geology Series 20: 137-157.

Gilmore, C.W. 1915. Osteology of *Thescelosaurus*, an orthopodous dinosaur from the Lance Formation of Wyoming. Proceedings of the United Stations National Museum 49: 591-616.

Hammer, Ø, and D. A. T. Harper. 2005. Paleontological Data Analysis, 1st ed. Wiley-Blackwell, pp. 83-91.

Hildebrand, M. 1985. Digging of quadrupeds. Functional Vertebrate Morphology 89–109.

Holliday, C. M., R. C. Ridgely, J. C. Sedlmayr, and L. M. Witmer. 2010. Cartilaginous epiphyses in extant archosaurs and their implications for reconstructing limb function in dinosaurs. PLoS One.

Horner, J. R., and D. B. Weishampel. 1988. A comparative embryological study of two ornithischian dinosaurs. Nature 322:256-257.

Horner, J. R., D. B. Weishampel, and C. A. Forster. 2004. Hadrosauridae. The Dinosauria 2:438–463.

Howell, A. B. 1937. Morphogenesis of the shoulder architecture: Aves. The Auk 54:364–375.

Huh, M., D. G. Lee, J. K. Kim, J. D. Lim, and P. Godefroit. 2010. A new basal ornithopod dinosaur from the Upper Cretaceous of South Korea. Neues Jahrbuch für Geologie und Paläontologie 259:1–24.

Kambic, R. E. 2008. Multivariate analysis of avian and non-avian theropod pedal phalanges. Montana State University Bozeman.

Kent, G. C., and R.K. Carr, 2008. Girdles, fins, limbs, and locomotion. Comparative Anatomy of the Vertebrates, 9th Ed. McGraw Hill Higher Education, pp. 199 – 232.

Kley, N. J., and M. Kearney. 2007. Adaptations for Digging and Burrowing; pp. 284–309 in Fins into limbs: evolution, development, and transformation. University of Chicago Press.

Longrich, N. R., and P. J. Currie. 2009. *Albertonykus borealis*, a new alvarezsaur (Dinosauria: Theropoda) from the Early Maastrichtian of Alberta, Canada: implications for the systematics and ecology of the Alvarezsauridae. Cretaceous Research 30:239–252.

Longrich, N. 2010. The function of large eyes in *Protoceratops*: a nocturnal ceratopsian. 308–327.

Maidment, S. C. R., and P. M. Barrett. 2011. The locomotor musculature of basal ornithischian dinosaurs. Journal of Vertebrate Paleontology 31:1265–1291.

Makovicky, P. J., B. M. Kilbourne, R. W. Sadleir, and M. A. Norell. 2011. A new basal ornithopod (Dinosauria, Ornithischia) from the Late Cretaceous of Mongolia. Journal of Vertebrate Paleontology 31:626–640.

Maloiy, G. M. O., R. Alexander, R. Njau, and A. S. Jayes. 1979. Allometry of the legs of running birds. Journal of Zoology 187:161–167.

Manly, B. F. J. 2005. Multivariate Statistical Methods: A Primer, Third Edition, 3rd ed. Chapman and Hall/CRC, pp. 105-124.

Martin, A. J. 2009. Dinosaur burrows in the Otway Group (Albian) of Victoria, Australia, and their relation to Cretaceous polar environments. Cretaceous Research 30:1223–1237.

Martin, A.J., M. Page, R.K. Vance, and S. Skaggs. 2012. Dens of the American alligator (*Alligator mississippiensis*) as traces and their predictive value for finding large archosaur burrows in the geologic record. Society of Vertebrate Paleontology: Program and Abstracts, 136.

Maxwell, E. E., and H. C. Larsson. 2007. Osteology and myology of the wing of the Emu (*Dromaius novaehollandiae*), and its bearing on the evolution of vestigial structures. Journal of Morphology 268:423–441.

McDonald, A.T., J.I. Kirkland, D.D. DeBlieux, S.K. Madsen, J. Cavin, A.R.C. Milner, and L. Panzarin. 2010. New basal iguanodonts from the Cedar Mountain formation of Utah and the evolution of thumb-spiked dinosaurs. PLoS ONE 5(11).

McGowan, C. 1982. The wing musculature of the Brown *Kiwi Apteryx* australis mantelli and its bearing on ratite affinities. Journal of Zoology 197:173–219.

McGowan, C. 1986. The wing musculature of the Weka (*Gallirallus australis*), a flightless rail endemic to New Zealand. Journal of Zoology 210:305–346.

Meers, M. B. 2003. Crocodylian forelimb musculature and its relevance to Archosauria. The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology 274:891–916.

Milne, N., S. F. Vizcaíno, and J. C. Fernicola. 2009. A 3D geometric morphometric analysis of digging ability in the extant and fossil cingulate humerus. Journal of Zoology 278:48–56.

Nicholls, E. L., and A. P. Russell. 1985. Structure and function of the pectoral girdle and forelimb of Struthiomimus altus (Theropoda: Ornithomimidae). Palaeontology 28:643–677.

Norman, D. B. 2004. Basal Iguanodontia. The Dinosauria 2:413–437.

Norman, D.B., H.D. Sues, L.M. Witmer, and R.A. Coria. 2004. Basal Ornithopoda. The Dinosauria 2: 393-419.

Norman, D.B, L.M. Witmer, and D.B. Weishampel. 2004. Basal Ornithischia. The Dinosauria 2: 325-334.

Parks, W. A. 1926. *Thescelosaurus warreni*, a new species of ornithopous dinosaur from the Edmonton Formation of Alberta. University of Toronto Studies Geology Series 21: 1-42.

Price, M. V. 1993. A functional-morphometric analysis of forelimbs in bipedal and quadrupedal heteromyid rodents. Biological Journal of the Linnean Society 50:339–360.

R Development Core Team. 2010. R Version 2.11.1 Available at http://www.r-project.org/

Reese, A. M. 1915. The Alligator and Its Allies. GP Putnam's Sons.

Rohlf, F.J. 2010a. TPSDig. Version 2.16. Available at http://life.bio.sunysb.edu/morph/

Rohlf, F.J. 2010b. TPS Relative Warps. Version 1.49. Available at http://life.bio.sunysb.edu/morph/

Rohlf, F.J. 2010c. TPS Utility Program. Version 1.46. Available at http://life.bio.sunysb.edu/morph/

Romer, A. S. 1944. The development of tetrapod limb musculature—the shoulder region of Lacerta. Journal of Morphology 74:1–41.

Scheetz, R. D. 1999. Osteology of *Orodromeus makelai* and the phylogeny of basal ornithopod dinosaurs. Montana State University–Bozeman pp.

Senter, P. 2005. Function in the stunted forelimbs of *Mononykus olecranus* (Theropoda), a dinosaurian anteater. Paleobiology 31:373.

Senter, P. 2007. Analysis of forelimb function in basal ceratopsians. Journal of Zoology 273:305–314.

Sereno, P. C. 2010. Noasaurid (Theropoda: Abelisauroidea) skeleton from Africa shows derived skeletal proportions and function. Society of Vertebrate Paleontology: Program and Abstracts, 2012, 162A.

Sheets, H.D. 2000. CoordGen6h. Available at http://www3.canisius.edu/~sheets/morphsoft.html

Sheets, H.D. 2006. CVAGen6o. Available at http://www3.canisius.edu/~sheets/morphsoft.html

Simpson, E. L., H. L. Hilbert-Wolf, M. C. Wizevich, S. E. Tindall, B. R. Fasinski, L. P. Storm, and M. D. Needle. 2010. Predatory digging behavior by dinosaurs. Geology 38:699.

Stokes, D. L., and P. D. Boersma. 1991. Effects of substrate on the distribution of Magellanic Penguin (*Spheniscus magellanicus*) burrows. The Auk 923–933.

Sues, H. D. 1980. Anatomy and relationships of a new hypsilophodontid dinosaur from the Lower Cretaceous of North America. Palaeontographica Abteilung A 169:51–72.

Thomsen, L. 1971. Behavior and ecology of burrowing owls on the Oakland Municipal Airport. The Condor 73:177–192.

Varricchio, D. J., A. J. Martin, and Y. Katsura. 2007. First trace and body fossil evidence of a burrowing, denning dinosaur. Proceedings of the Royal Society B: Biological Sciences 274:1361–1368.

Vizcaíno, S. F., R. A. Fariña, and G. V. Mazzetta. 1999. Ulnar dimensions and fossoriality in armadillos. Acta Theriologica 44:309–320.

Waas, J. R. 1990. An analysis of communication during the aggressive interactions of little blue penguins (*Eudyptula minor*). Penguin Biology 345–373.

Weishampel, D. B., R. E. Chapman, K. Carpenter, and P. J. Currie. 1990. Morphometric study of Plateosaurus from Trossingen (Baden-Wurttemberg, Federal Republic of Germany). Dinosaur Systematics: Approaches and Perspectives. pp. 43–51.

Witmer, L. M., and J. J. Thomason. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. Functional Morphology in Vertebrate Paleontology 1:19–33.

Woodruff, D. C., and D. J. Varricchio. 2011. Experimental modeling of a possible *Oryctodromeus cubicularis* (Dinosauria) burrow. Palaios 26:140–151.

Yasuda, M. 2002. The Anatomical Atlas of *Gallus*. University of Tokyo Press, pp. 155-240

Zelditch, M. L., D. L. Swiderski, and H. D. Sheets. 2012. Geometric Morphometrics for Biologists, Second Edition: A Primer, 2nd ed. Academic Press, pp. 155-187.

APPENDICES

APPENDIX A

SPECIMEN LISTS

Table 1. Specimens included in the traditional morphometric analysis of the humerus.

Specimen	Taxon	Group	Notes:
BYU 631-163	*Othnielosaurus consors*	Basal Ornithischia	
BYU 16719	*Othnielosaurus sp.*	Basal Ornithischia	
BMNH RU B.17	*Lesothosaurus diagnosticus*	Basal Ornithischia	
MOR 1642	*Oryctodromeus cubicularis*	Basal Ornithopod	
MOR 1642	*Oryctodromeus cubicularis*	Basal Ornithopod	
MOR 1642	*Oryctodromeus cubicularis*	Basal Ornithopod	
MOR 1636	*Oryctodromeus cubicularis*	Basal Ornithopod	
MOR 1636	*Oryctodromeus cubicularis*	Basal Ornithopod	Juvenile
IMNH 44951	*Oryctodromeus cubicularis*	Basal Ornithopod	
MOR 623	*Orodromeus makelai*	Basal Ornithopod	
MOR 404	*Orodromeus makelai*	Basal Ornithopod	
MOR 294	*Orodromeus makelai*	Basal Ornithopod	Juvenile
MOR 473	*Orodromeus makelai*	Basal Ornithopod	
HC-164	*Thescelosaurus sp.*	Basal Ornithopod	cast.
CM 9900	*Thescelosaurus neglectus*	Basal Ornithopod	
BMNH R192	*Hypsilophodon foxii*	Basal Ornithopod	
BMNH R194	*Hypsilophodon foxii*	Basal Ornithopod	
BMNH R196	*Hypsilophodon foxii*	Basal Ornithopod	Same individual as below
BMNH R196	*Hypsilophodon foxii*	Basal Ornithopod	
BMNH R5830	*Hypsilophodon foxii*	Basal Ornithopod	Small individual, not described as juvenile.
FMNH IGM	*Haya griva*	Basal Ornithopod	cast.

100/2015			
MOR 548	Lambeosaur	Hadrosauridae	Juvenile
MOR 548	Lambeosaur	Hadrosauridae	Juvenile
MOR 548	Lambeosaur	Hadrosauridae	Juvenile
MOR 548	Lambeosaur	Hadrosauridae	Juvenile
MOR 548	Lambeosaur	Hadrosauridae	Juvenile
MOR 548	Lambeosaur	Hadrosauridae	Juvenile
MOR 548	Lambeosaur	Hadrosauridae	Juvenile
MOR 547	*Maiasaura peeblesorum*	Hadrosauridae	Subadult
MOR 547	*Maiasaura peeblesorum*	Hadrosauridae	Subadult
YPM-PU 22400	*Maiasaura peeblesorum*	Hadrosauridae	Juvenile
YPM-PU 22400	*Maiasaura peeblesorum*	Hadrosauridae	Juvenile
YPM-PU 23444	*Maiasaura sp.*	Hadrosauridae	Juvenile
MOR 478	*Grypsosaurus latidens*	Hadrosauridae	
MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	
MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	
MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	
MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	
MOR 311	Hadrosaurine	Hadrosauridae	
YPM-PU 23255	Hadrosaur	Hadrosauridae	
MOR 607	Hadrosaur	Hadrosauridae	
YPM 3454	Hadrosaur	Hadrosauridae	
CM 1066	Hadrosaur indet.	Hadrosauridae	
CM 30745	*Edmontosaurus sp.*	Hadrosauridae	
BMNH R3640	*"Trachodon sp."*	Hadrosauridae	
CM 9461	*Corythosaurus casuarius*	Hadrosauridae	
DBDP-42	Unnamed Iguanodontian	Iguanodontia	
DBJP-119	Unnamed Iguanodontian	Iguanodontia	
DBDP-163b	Unnamed Iguanodontian	Iguanodontia	
UMNH VP20208	*Hippodraco*	Iguanodontia	

	scutodens		
BYU 17945	*Camptosaurus sp.*	Iguanodontia	
CM 11337	*Camptosaurus aphanoecetes*	Iguanodontia	Same individual as below.
CM 11337	*Camptosaurus aphanoecetes*	Iguanodontia	
YPM 1877	*Camptosaurus dispar*	Iguanodontia	
YPM 1800	*Camptosaurus dispar*	Iguanodontia	Same individual as below.
YPM 1800	*Camptosaurus dispar*	Iguanodontia	
YPM 6794	*Camptosaurus medius*	Iguanodontia	
YPM 7331	*Camptosaurus medius*	Iguanodontia	
YPM 5456	*Tenontosaurus tilletti*	Iguanodontia	
YPM-PU 16514	*Tenontosaurus tilletti*	Iguanodontia	
YPM 5456	*Tenontosaurus tilletti*	Iguanodontia	
FMNH PR2263	*Tenontosaurus tilletti*	Iguanodontia	Juvenile
MOR 2558	*Tenontosaurus tilletti*	Iguanodontia	
CM 3392	*Dryosaurus altus*	Iguanodontia	
CM3392/21786	*Dryosaurus altus*	Iguanodontia	Same individual as below.
CM3392/21786	*Dryosaurus altus*	Iguanodontia	
YPM 1876	*Dryosaurus altus*	Iguanodontia	
BYU 5215	*Dryosaurus sp.*	Iguanodontia	
CM 21786	*Dryosaurus sp.*	Iguanodontia	
CM 9185	*Protoceratops andrewsi*	Marginocephalia	
FMNH IGM 100/1930	*Psittacosaurus mongoliensis*	Marginocephalia	
UofC LHPV2	*Psittacosaurus gobiensis*	Marginocephalia	Same individual as below.
UofC LHPV2	*Psittacosaurus gobiensis*	Marginocephalia	

Table 2. Specimens used in the traditional morphometric analysis of the scapula.

Specimen	Taxon	Group	Notes:
BYU 631-163	*Othnielosaurus consors*	Basal Ornithischia	
BMNH R11000	*Stormbergia dangershoeki*	Basal Ornithischia	
BMNH RU B.17	*Lesothosaurus diagnosticus*	Basal Ornithischia	
MOR1636	*Oryctodromeus cubicularis*	Basal Ornithopod	Same individual as below, Fused scapulocoracoid
MOR1636	*Oryctodromeus cubicularis*	Basal Ornithopod	Unfused
MOR 1636	*Oryctodromeus cubicularis*	Basal Ornithopod	Juvenile, Unfused scapulocoracoid
MOR 1642	*Oryctodromeus cubicularis*	Basal Ornithopod	Fused
MOR 294	*Orodromeus makelai*	Basal Ornithopod	Juvenile
MOR 623	*Orodromeus makelai*	Basal Ornithopod	
UMNH VP20644	Unnamed Hypsilophodontid	Basal Ornithopod	
BMNH R192	*Hypsilophodon foxii*	Basal Ornithopod	
BMNH R196	*Hypsilophodon foxii*	Basal Ornithopod	
BMNH R196	*Hypsilophodon foxii*	Basal Ornithopod	Small individual.
FMNH IGM 100/2015	*Haya griva*	Basal Ornithopod	Fused scapulocoracoid
MOR 547 W-25-2	*Maiasaura peeblesorum*	Hadrosauridae	
BYU 12192	Hadrosaur	Hadrosauridae	
MOR 584	Lambeosaur	Hadrosauridae	Juvenile
MOR 584	Lambeosaur	Hadrosauridae	Juvenile
MOR 584	Lambeosaur	Hadrosauridae	Juvenile
YPM-PU 22503	Lambeosaurine indet.	Hadrosauridae	
MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	
CM 9461	*Corythosaurus casuarius*	Hadrosauridae	
BYU 17948	*Camptosaurus sp.*	Iguanodontia	

BYU 17945	*Camptosaurus sp.*	Iguanodontia	
UMNH VP16567	*Camptosaurus sp.*	Iguanodontia	
CM 11337	*Camptosaurus aphanoecetes*	Iguanodontia	Same individual as below.
CM 11337	*Camptosaurus aphanoecetes*	Iguanodontia	
YPM 1877	*Camptosaurus dispar*	Iguanodontia	Cast.
YPM 56454	*Camptosaurus dispar*	Iguanodontia	
YPM 1800	*Camptosaurus dispar*	Iguanodontia	Same individual as below.
YPM 1800	*Camptosaurus dispar*	Iguanodontia	
YPM 8611	*Camptosaurus medius*	Iguanodontia	
DBDP-185	Unnamed Iguanodontian	Iguanodontia	
UMNH VP20208	*Hippodraco scutodens*	Iguanodontia	
MOR 682	*Tenontosaurus tilletti*	Iguanodontia	
YPM 5456	*Tenontosaurus tilletti*	Iguanodontia	Same individual as below.
YPM 4546	*Tenontosaurus tilletti*	Iguanodontia	
CM3392/21786	*Dryosaurus altus*	Iguanodontia	Same individual as below.
CM3392/21786	*Dryosaurus altus*	Iguanodontia	
BMNH R2519	*Iguanodon sp.*	Iguanodontia	
BMNH R2196	*Iguanodon mantelli*	Iguanodontia	
BMNH R966	*Iguanodon dawsoni*	Iguanodontia	
BMNH R4743	*Iguanodon titanni*	Iguanodontia	
CM 9185	*Protoceratops andrewsi*	Marginocephalia	
FMNH IGM 100/1930	*Psittacosaurus mongoliensis*	Marginocephalia	
UofC LHPV2	*Psittacosaurus gobiensis*	Marginocephalia	Same individual as below.
UofC LHPV2	*Psittacosaurus gobiensis*	Marginocephalia	

Table 3. Specimens used in the traditional morphometric analysis of the coracoid.

Specimen	Taxon	Group	Notes:
BYU 631-163	*Othnielosaurus consors*	Basal Ornithischia	
BMNH R11000	*Stormbergia dangershoeki*	Basal Ornithischia	
MOR 1636	*Oryctodromeus cubicularis*	Basal Ornithopod	Fused scapulocoracoid
MOR 1642	*Oryctodromeus cubicularis*	Basal Ornithopod	Unfused scapulocoracoid
MOR 623	*Orodromeus makelai*	Basal Ornithopod	
BMNH R192	*Hypsilophodon foxii*	Basal Ornithopod	
BMNH R196	*Hypsilophodon foxii*	Basal Ornithopod	
BMNH R196	*Hypsilophodon foxii*	Basal Ornithopod	
FMNH IGM 100/2015	*Haya griva*	Basal Ornithopod	cast, Fused scapulocoracoid
CM 9461	*Corythosaurus casuarius*	Hadrosauridae	
UMNH VP16422	*Camptosaurus sp.*	Iguanodontia	
YPM 1877	*Camptosaurus dispar*	Iguanodontia	
YPM 1800	*Camptosaurus dispar*	Iguanodontia	Same individual as below.
YPM 1800	*Camptosaurus dispar*	Iguanodontia	
CM 11337	*Camptosaurus aphanoecetus*	Iguanodontia	Same individual as below.
CM 11337	*Camptosaurus aphanoecetus*	Iguanodontia	
YPM 5478	*Tenontosaurus tilletti*	Iguanodontia	
YPM 5456	*Tenontosaurus tilletti*	Iguanodontia	
CM3392/21786	*Dryosaurus altus*	Iguanodontia	Same individual as below.
CM3392/21786	*Dryosaurus altus*	Iguanodontia	
CM 9185	*Protoceratops andrewsi*	Marginocephalia	
UofC LHPV2	*Psittacosaurus gobiensis*	Marginocephalia	

Table 4. Specimens used in the geometric morphometric analysis of the humerus.

Specimen	Taxon	Group	Notes:
BYU 16719	*Othnielosaurus sp.*	Basal Ornithischia	
BMNH B.17	*Lesothosaurus diagnosticus*	Basal Ornithischia	
IMNH 44951	*Oryctodromeus cubicularis*	Basal Ornithopoda	
MOR 1636	*Oryctodromeus cubicularis*	Basal Ornithopoda	
MOR 1642	*Oryctodromeus cubicularis*	Basal Ornithopoda	
MOR 1642	*Oryctodromeus cubicularis*	Basal Ornithopoda	
MOR 1636	*Oryctodromeus cubicularis*	Basal Ornithopod	Juvenile
MOR 294	*Orodromeus makelai*	Basal Ornithopoda	Juvenile
MOR 404	*Orodromeus makelai*	Basal Ornithopoda	
MOR 473	*Orodromeus makelai*	Basal Ornithopoda	
MOR 623	*Orodromeus makelai*	Basal Ornithopoda	
BMNH R194	*Hypsilophodon foxii*	Basal Ornithopoda	
BMNH R196	*Hypsilophodon foxii*	Basal Ornithopoda	
BMNH R196	*Hypsilophodon foxii*	Basal Ornithopoda	
BMNH R5830	*Hypsilophodon foxii*	Basal Ornithopoda	
CM 9900	*Thescelosaurus sp.*	Basal Ornithopoda	
MOR HC-164	*Thescelosaurus sp.*	Basal Ornithopoda	
FMNH IGM 100/2015	*Haya griva*	Basal Ornithopod	Cast
CM 9461	*Corythosaurus casuarius*	Hadrosauridae	
MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	
MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	
MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	
MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	
MOR 478	*Grypsosaurus latidens*	Hadrosauridae	
MOR 547	*Maiasaura*	Hadrosauridae	

	peeblesorum		
MOR 547	*Maiasaura peeblesorum*	Hadrosauridae	
MOR 548	Lambeosaur indet.	Hadrosauridae	Juvenile
MOR 548	Lambeosaur indet.	Hadrosauridae	Juvenile
MOR 548	Lambeosaur indet.	Hadrosauridae	Juvenile
MOR 548	Lambeosaur indet.	Hadrosauridae	Juvenile
MOR 607	Hadrosaur indet.	Hadrosauridae	
CM 30745	*Edmontosaurus sp. ("Anatosaurus sp.")*	Hadrosauridae	
BMNH R3640	*Edmontosaurus sp. ("Trachodon sp.")*	Hadrosauridae	
YPM-PU 23255	Hadrosaur indet.	Hadrosauridae	
YPM 3454	Hadrosaur indet.	Hadrosauridae	
MOR 311	Hadrosaur indet.	Hadrosauridae	
CM 1066	Hadrosaur indet.	Hadrosauridae	
BYU 5215	*Dryosaurus sp.*	Iguanodontia	
CM 21786	*Dryosaurus sp.*	Iguanodontia	
CM 3392	*Dryosaurus altus*	Iguanodontia	
YPM 1876	*Dryosaurus altus*	Iguanodontia	
CM3392/21786	*Dryosaurus altus*	Iguanodontia	
DBDP-163b	Unnamed Iguanodontian	Iguanodontia	
DBDP-42	Unnamed Iguanodontian	Iguanodontia	
DPJP-119	Unnamed Iguanodontian	Iguanodontia	
MOR 2558	*Tenontosaurus tilletti*	Iguanodontia	
YPM 5456	*Tenontosaurus tilletti*	Iguanodontia	
YPM 5456	*Tenontosaurus tilletti*	Iguanodontia	
YPM-PU 16514	*Tenontosaurus tilletti*	Iguanodontia	
BMNH R116	*Iguanodon mantelli*	Iguanodontia	
CM 11337	*Camptosaurus aphanoecetes*	Iguanodontia	
YPM 1800	*Camptosaurus dispar*	Iguanodontia	
YPM 1877	*Camptosaurus dispar*	Iguanodontia	
YPM 1878	*Camptosaurus*	Iguanodontia	

	dispar	
YPM 6794	*Camptosaurus medius*	Iguanodontia
YPM 7331	*Camptosaurus medius*	Iguanodontia
CM 9185	*Protoceratops andrewsi*	Marginocephalia
UofC LHVP2	*Psittacosaurus gobiensis*	Marginocephalian

Table 5. Specimens used in the geometric morphometric analysis of the scapula.

Specimen	Taxon	Group	Notes:
BYU 163	*Othnielosaurus consors*	Basal Ornithischia	
BMNH R11000	*Stormbergia dangershoeki*	Basal Ornithischia	
MOR 623	*Orodromeus makelai*	Basal Ornithopod	
MOR 294	*Orodromeus makelai*	Basal Ornithopod	Juvenile
MOR 1636	*Oryctodromeus cubicularis*	Basal Ornithopod	Unfused
MOR 1636	*Oryctodromeus cubicularis*	Basal Ornithopod	Fused
MOR 1636	*Oryctodromeus cubicularis*	Basal Ornithopod	Juvenile
MOR 1642	*Oryctodromeus cubicularis*	Basal Ornithopod	Fused
BMNH R192	*Hypsilophodon foxii*	Basal Ornithopod	
BMNH R196	*Hypsilophodon foxii*	Basal Ornithopod	
YPM 56454	*Hypsilophodontid indet.*	Basal Ornithopod	
FMNH IGM 100/2015	*Haya griva*	Basal Ornithopod	Cast
CM 9461	*Corythosaurus casuarius*	Hadrosauridae	
MOR 548	Lambeosaur indet.	Hadrosauridae	
MOR 548	Lambeosaur indet.	Hadrosauridae	
MOR 547	*Maiasaura peeblesorum*	Hadrosauridae	
MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	

MOR 1071	*Brachylophosaurus canadensis*	Hadrosauridae	
BYU 17945	*Camptosaurus sp.*	Iguanodontia	
BYU 17948	*Camptosaurus sp.*	Iguanodontia	
UMNH VP 16567	*Camptosaurus sp.*	Iguanodontia	
YPM 1800	*Camptosaurus dispar*	Iguanodontia	
YPM 1877	*Camptosaurus dispar*	Iguanodontia	Cast.
YPM 8611	*Camptosaurus dispar*	Iguanodontia	
CM 11337	*Camptosaurus aphanoecetes*	Iguanodontia	Same individual as below.
CM 11337	*Camptosaurus aphanoecetes*	Iguanodontia	
CM3392/21786	*Dryosaurus altus*	Iguanodontia	
UMNH VP20208	*Hippodraco scutodens*	Iguanodontia	
BMNH R2196	*Iguanodon mantelli*	Iguanodontia	
BMNH 4743	*Iguanodon titanni*	Iguanodontia	
BMNH R966	*Iguanodon dawsoni*	Iguanodontia	
YPM 5456	*Tenontosaurus tilletti*	Iguanodontia	
YPM 5456	*Tenontosaurus tilletti*	Iguanodontia	
MOR 682	*Tenontosaurus tilletti*	Iguanodontia	
CM 9185	*Protoceratops andrewsi*	Marginocephalian	
UofC LHVP2	*Psittacosaurus gobiensis*	Marginocephalian	Same individual as below.
UofC LHVP2	*Psittacosaurus gobiensis*	Marginocephalian	

Table 6. Specimens used in the geometric morphometric analysis of the coracoid.

Specimen	Taxon	Group	Notes:
BYU 163	*Othnielosaurus sp.*	Basal Neornithischian	
BMNH R11000	*Stormbergia dangershoeki*	Basal Neornithischian	Fused.
FMNH IGM 100/2015	*Haya griva*	Basal Ornithopod	Cast.
IMNH 44951	*Oryctodromeus cubicularis*	Basal Ornithopod	Unfused.
MOR 1636	*Oryctodromeus cubicularis*	Basal Ornithopod	Fused.

MOR 623	*Orodromeus makelai*	Basal Ornithopod	
BMNH R196	*Hypsilophodon foxii*	Basal Ornithopod	
CM3392	*Dryosaurus altus*	Iguanodontian	Same individual as below.
CM3392	*Dryosaurus altus*	Iguanodontian	
CM 11337	*Camptosaurus aphanoecetes*	Iguanodontian	Same individual as below.
CM 11337	*Camptosaurus aphanoecetes*	Iguanodontian	
UMNH VP 16422	*Camptosaurus sp.*	Iguanodontian	
YPM 1800	*Camptosaurus dispar*	Iguanodontian	Same individual as below.
YPM 1800	*Camptosaurus dispar*	Iguanodontian	
YPM 1877	*Camptosaurus dispar*	Iguanodontian	
YPM 5478	*Tenontosaurus tilletti*	Iguanodontian	
YPM 5654	*Tenontosaurus tilletti*	Iguanodontian	
FMNH IGM 100/1930	*Psittacosaurus mongoliensis*	Marginocephalian	
CM9185	*Protoceratops andrewsi*	Marginocephalian	

APPENDIX B

FORELIMB DESCRIPTION, EXCERPT FROM *ORYCTODROMEUS* MANUSCRIPT (KRUMENACKER ET AL., UNPUBLISHED)

Coracoid

Coracoids are well represented among *Oryctodromeus* elements. BYU 19343 preserves one coracoid, BYU 19342 preserves coracoid fragments, and BYU 19345 has a partial coracoid. MOR 1636a preserves one fused right scapulocoracoid, and one unfused left coracoid. MOR 1636b preserves one unfused left coracoid. MOR 1642 preserves a left and right coracoid fused with their respective scapulae.

The coracoid extends anteriorly from the scapula and is relatively large, elongate dorsoventrally, and robust; with an ovoid outline similar to that of *Orodromeus* (Fig. 10A-B; Scheetz, 1999). The anteriormost margin of the coracoid curves medially, but otherwise the coracoid is nearly flat. The scapular articulation is thin and buttressed posteriorly by a transverse expansion with a large glenoid cavity bearing a centrally placed glenoid fossa which extends ventrally. The coracoid is thickest along the scapulocoracoid fusion, near the glenoid; the scapular fusion thins dorsally from the glenoid, towards the acromion of the scapula. The coracoid foramen is placed well anterior of the scapula and fully enclosed within the coracoid, unlike *Hypsilophodon* (Fig. 10A; Galton, 1974). The foramen appears circular on the lateral surface, but is more elongate medially and in some specimens a shallow linear depression extends from the coracoid foramen towards the scapular articulation. As in *Orodromeus* (Scheetz, 1999), the sternal process is prominent, making the posterior border of the coracoids strongly concave. In some specimens, a shallow, elongate, ovoid fossa (referred to here as the ventral fossa) is located ventrally, between the sternal process and the glenoid fossa. In BYU 19343, another shallow, circular fossa (referred to here as the lateral fossa) is present on the lateral surface of the coracoid, located dorsal to the ventral fossa.

The coracoid of a juvenile specimen (MOR 1636b) greatly resembles that of the adult *Orodromeus*; it is more circular in general shape than the adult *Oryctodromeus* coracoid. The juvenile coracoid is not as concave medially, and is not thickened near the glenoid, unlike the adult *Oryctodromeus* specimen.

Sternum

No sternal material has been identified for *Oryctodromeus*.

Scapula

The scapulae of Blackleaf Formation *Oryctodromeus* specimens are unique in that they are fused with the coracoid in some known adult specimens. Both the left and right scapulocoracoids of MOR 1642 and the left scapulocoracoid of MOR 1636a are fused; however the right scapula of MOR 1636a is unfused, as is the scapula of MOR 1636b. For clarity of description, the scapula will be described with the blade oriented horizontally, in the same manner as *Orodromeus* (Scheetz, 1999).

The scapular blade is thin when viewed ventrally or dorsally, and the expanded anterior end curves medially. Laterally, the anterior end of the scapula is deeply concave between the scapular spine and the glenoid. The ventral region of the anterior scapula is thickened near the glenoid. The acromion process is prominently angled with a laterally projecting scapular spine similar in angle and form to *Orodromeus* (Scheetz, 1999), *Zephyrosaurus*, and *Koreanosaurus* (Huh *et al*., 2010). The scapular spine extends from the anterodorsal-most corner of the scapula posteroventrally, meeting with the thickened region posterodorsal to the glenoid. The scapular spine is tall and extends laterally. In cross-section, the anterior region of the scapular spine is asymmetrical, with a gradual dorsal slope back to the plane of the scapula but a steep ventral slope. Posteriorly the

cross-section becomes more symmetrical. The scapular spine is reduced to a thickening which continues on the scapular blade, resulting in the slightly convex lateral surface of the scapular blade. The blade is relatively shorter anteroposteriorly and taller dorsoventrally than that of *Orodromeus* (Scheetz, 1999). The dorsal edge of the scapular blade is relatively short and straight, extending roughly perpendicular to the scapular spine. It forms a roughly 135^{o} angle with the posterior edge of the scapular blade at the superior angle. The posterior edge is broad and convex, and is expanded ventrally, similar to, but to a greater extent than *Orodromeus* (Scheetz, 1999). At the superior angle, the posterior edge of the blade is thin but thickens ventrally. The lateral surface of the margin of the posterior blade has a roughened surface, which is indicative of muscle scarring. The inferior angle is sharp, forming an acute angle with the ventral edge. The ventral edge of the scapular blade is highly concave, ending anteriorly at the scapular side of the glenoid. The glenoid faces ventrally and is bisected by the fusion of the scapula and coracoid. The scapular and coracoid portions of the glenoid come together at a roughly 90^{o} angle, and are roughly square and equal in size.

The shape of the scapula varies slightly between the adult and juvenile specimens. The scapular glenoid faces slightly ventrolaterally, rather than ventrally. The scapular spine appears less developed in the juvenile specimen, however, most of the acromion was not preserved, so it is unclear how the scapular spine and acromion change during ontogeny. The scapular blade is proportionally longer relative to the dorsoventral height in the juvenile specimen.

Humerus

MOR 1636a preserves a right humerus, MOR 1636b preserves a left humerus, and MOR 1642 preserves two right humeri, one with a crushed proximal end, and one left humerus. Two fragmentary and three nearly complete humeri are known from the Wayan Formation and compare favorably to the complete humeri of the holotype and paratype (MOR 1636a & 1636b). Near complete specimens are known from BYU 19344 and BYU 19345, while a proximal portion is known from BYU 19342 and fragments from BYU 19347. The best Wayan Formation specimen is a complete left humerus associated with 19343. Here descriptions are based on BYU 19343, BYU 19342, and BYU 19344.

In lateral and posterior view, the humerus is sigmoidal. Proximally the humerus is expanded into the humeral head, with the deltopectoral crest extending anteriorly from the proximal third of the humerus, with the proximal third of the humerus concave anteromedially. Distal to the deltopectoral crest, the shaft of the humerus narrows, then expands again into a bicondylar distal end. The deltopectoral crest extends about one third the length of the humerus from the proximal end. The apex of the deltopectoral crest has a rough texture. Lateral to the apex of the deltopectoral crest is a slightly concave, smooth surface. The deltopectoral crest thins and shortens beyond the apex, along its distal margin. The shaft of the humerus is slightly oval in cross section, expanded anteroposteriorly immediately distal to the deltopectoral crest, but twists distally to be transversely expanded. The distal end of the humerus is bicondylar, with a rougher surface than the generally smooth shaft. The ulnar condyle is medial and slightly wider and larger than the smaller, more anterolateral radial condyle. The two condyles

are separated by an intercondylar groove which is more evident on the strongly concave anterior surface. In distal view, the humerus is dumbbell shaped.

Ulna

The right ulna is preserved in MOR 1642, and the left ulna is preserved in MOR 1636a; no juvenile ulnae were preserved. Two ulnae are known from the Wayan, the proximal and possible distal ends of BYU 19347, and one from BYU 19345. This description is based on MOR 1642 and BYU 19345, and BYU 19347.

The ulna is slightly bowed in shape and is longer than the radius. The proximal end of the ulna is expanded and triangular in dorsal view, with a flat articular surface for the ulnar condyle of the humerus. The olecranon process extends proximally, posterior to the humeral articular surface of the ulna. The olecranon process is more pronounced in *Oryctodromeus* than in *Hypsilophodon* (Galton, 1974) and *Orodromeus* (Scheetz, 1999). The proximal surface anterior to the olecranon is slightly concave for articulation with the ulnar condyle. The ulna is widest at its proximal end and narrows rapidly in the proximal fourth of its length. The medial surface of the proximal shaft is slightly concave, with a slightly rough articular surface for the radius distal to the olecranon, and a small concave facet anteriorly. The shaft is roughly triangular to oval in cross-section, and nearly as robust as the humerus at its most narrow. In BYU 19345, the ulna is over 80% the length of the humerus.

Radius

The right radius is preserved in MOR 1642, and a left radius is preserved in MOR 1636a. Both are used for the description here.

The distal portions of both radii are crushed, but the proximal ends are well preserved. The radius has a straight shaft and slightly expanded distal and proximal ends. The proximal end is reniform, and elongate anteroposteriorly, with the convex edge facing laterally and the concave edge facing medially. The radial tuberosity is present as a small protuberance which articulates with the concave facet on the ulna located on the anterior medial edge of the proximal radius. The proximal surface has a slightly convex surface, with a concavity in the center. The shaft of the radius is roughly triangular and smooth.

Manus

The manus material of Blackleaf *Oryctodromeus* specimens is disarticulated, and many elements are not represented in the material. A partial articulated manus is preserved in BYU 19345. Tentatively, these metacarpals are assigned as II, III, IV, and V and are/were present (II was only an imprint that was inadvertently removed during preparation). The MOR manus material includes the intermedium and one other carpal, metacarpals III and V, and four manual phalanges from MOR 1642; no manus material is known from MOR 1636. This description is based on BYU 19345 and MOR 1642.

In BYU 19345 the longest metacarpal (metacarpal III?) is 23% the length of the ulna; proximally metacarpal IV is expanded, and III to a lesser degree. In this specimen, metacarpals III and II are elongate and slender, similar to those of *Dryosaurus* (Galton, 1981) and *Hypsilophodon* (Galton, 1974).

The intermedium is roughly cubical and has a transversely convex and proximodistally concave dorsal surface opposite a concave ventral surface. Both of these surfaces have a smooth finish resembling a polish, and are darker in color than the other

surfaces of the intermedium. The remaining four surfaces are not polished. The proximal surface in articulation with the radius is deeply concave, while the articular surface with the ulna is flat. The distal surfaces are slightly convex. The other carpal - likely the radiale or ulnare, based on the *Hypsilophodon* manus description (Galton, 1974) - is roughly cubic, with a single polished surface which is slightly concave in one direction, and slightly convex perpendicularly. The other surfaces are all slightly convex and unpolished. The surface opposite the polished surface is smaller than its opposite. Metacarpal III is the longest of the known metacarpals, and has slightly expanded proximal and distal ends. The proximal end is slightly wider transversely than it is tall. What is tentatively identified as the palmar surface of the proximal half of Metacarpal III is concave. The distal end is weakly bicondylar, with a roughly flat dorsal surface, and a slight concavity ventrally. The lateral and medial faces of the condyles are slightly concave. Metacarpal V is shorter with a convex, wider-than-tall proximal end, and a more square convex distal end.

Four manual phalanges, three proximal and one distal, are preserved, but no ungual phalanges are known for *Oryctodromeus*. Based on the manus illustration in Galton (1974), the phalanges appear to be from digits II or III. The proximal phalanges are proximally and distally expanded; they exhibit very slightly concave proximal ends and bicondylar distal ends with weakly concave lateral and medial collateral ligament pits. The distal phalanx is shorter than the proximal phalanges; the proximal end exhibits two concavities for articulation with a more proximal phalanx, and the distal end is not transversely expanded, and has slightly concave lateral and medial collateral ligament pits.

APPENDIX C

MEASUREMENTS FOR THE TRADITIONAL MORPHOMETRIC ANALYSIS

Table 1. Measurements used in the traditional morphometric analysis of the humerus. Abbreviations described in Table 3.1

ID#	HL	DPL	DPW	HHW	HPW	HSW	HSP	HDW	RCW	UCW
MOR 1642	157.66	56.7	4.74	17.52	39.15	14.98	15.44	23.51	18.05	15.52
MOR 1642	160.87	60	4.82	20.99	33.26	15.54	14.35	21.05	18.47	13.25
MOR 1636	157.5	57.08	5.51	23.05	43.02	15.35	15.72	25.83	20.05	20.26
MOR 1642	168.81	66.8	4.44	17	38.39	14.17	14.99	25.7	17.81	15.9
MOR 623	92.89	32.46	3.38	9.17	24.27	7.37	10.76	11.94	13.26	12.8
BYU 631-163	104.27	32.67	3.59	13.32	25.93	11.44	9.23	18.8	15.05	13.07
BYU 16719	98.64	42.28	4.06	13.15	26.36	10.97	9.86	21.09	11.35	10.13
BYU 5215	200	75.94	9.76	19.89	56.08	20.64	17.42	35.33	19.15	18.58
BYU 17945	248	71.11	15.12	31.77	75.82	30.85	21.35	54.49	26.8	28.21
IMNH 44951	132.58	51.09	5.43	15.01	38.82	13.25	13.04	24.47	14.18	12.69
DBDP-42	298	121.9	14.17	31.56	80.23	32.4	29.46	54.68	28.2	35.59
DBJP-119	306	105.98	9.34	31.95	89.29	39.37	27.62	60.22	37.33	39.29
DBDP-163b	265	101.13	17.7	22.23	72.45	29.18	24.89	49.39	34.3	26.43
UMNH VP20208	334	127.62	9.95	43.22	74.98	24.18	43.3	42.72	48.1	49.8
MOR 548	107.51	47.41	4.77	14.13	34.16	14.93	12.73	29.93	16.08	15.21
MOR 548	114.18	54.2	6.04	15.62	38.51	15.26	16.41	30.17	15.86	16.16
MOR 548	115.07	47.5	6.6	19.94	39.13	17.31	15.94	32.52	13.95	18.26
MOR 548	118.69	50.93	7.01	11.95	39.94	16.46	16.19	29.78	11.4	10.04
MOR 548	128.86	57.61	6.4	14.93	43.59	18.09	18.21	34.83	15.52	18.05
MOR 548	120.14	53.57	4.92	14.11	39.93	14.97	17.18	25.82	15.42	18.04
MOR 548	123.57	60.12	5.48	15	38.95	16.65	17.99	29.91	19.69	17.48
MOR 547	239	110.26	10.51	21.29	51.43	24.74	26.53	34.52	29.65	34.97
MOR 547	245	113.61	8.28	31.1	55.47	25.43	25.62	45.44	32.17	36.63
MOR 404	70.14	22.61	4.36	11.53	21.23	6.58	6.35	14.35	10.3	9.87
MOR 294	63.64	19.7	3.57	8.84	18.69	6.31	7.45	11.98	9.27	9.75
MOR 473	104.44	39.96	3.66	14.47	30.06	10.85	10.2	20.34	15.93	15.47
MOR 478	570	254	26.26	49.17	140.13	57.9	43.51	87.65	70.15	79.91
MOR 607	283	143.77	8.95	42.99	64.68	25.31	46.04	50.3	37.05	46.05
HC-164	198	60.47	6.91	26.27	59.49	22.01	18.25	36.57	27.16	24.38
MOR 311	611	308	29.83	89.19	178	77.05	61.87	131.89	88.49	97.5
MOR 1071	355	170	20.85	44.93	100.07	38.96	45.24	76.8	43.85	48.41
MOR 1071	354	174	21.07	49.77	91.93	37.89	44.47	74.75	45.45	51.66
MOR 1071	381	170	21.4	55.97	97.47	39.84	52.67	84.09	47.32	57.82
MOR 1071	563	265	31.05	57.3	154	73.21	50.06	122.88	75.33	83.05
MOR 2558	462	177	30.85	61.84	173	71.85	41.39	138.03	75.99	73.72
YPM 1876	187	74.84	11.77	29.93	56.52	19.31	20.5	43.36	25.12	25.44
YPM 6794	236	116.08	21.96	47.72	84.02	36.33	30.52	67.08	39.3	38.82

YPM 7331	229	85.78	17.94	31.7	73.55	28.96	25.77	56.31	31.35	31.98
YPM 1877	339	129	20.27	53.88	108.83	29.55	27.77	85.01	48.49	44.86
YPM 5456	440	182	29.04	87.2	145.61	52.23	57.6	123.07	71.7	74.35
YPM-PU 16514	200	81.17	5.21	26.57	61.9	27.23	23.45	49.95	28.49	26.79
YPM 5456	447	178	23.44	69.26	153.97	56.96	52.71	116.05	66.6	73.81
YPM-PU 23255	537	246	27.16	50.37	157	65.61	52.91	116.5	75.85	78.78
YPM-PU 22400	81.36	35.46	4.25	10.85	20.74	9.48	8.89	18.29	9.71	9.4
YPM 3454	359	183	20.29	45.04	93.4	47.36	44.32	84.79	46.94	58.94
YPM-PU 23444	107.2	47.86	7.74	14.27	31.64	15.64	17.5	27.67	14.06	17.25
YPM-PU 22400	75.29	35.42	2.98	8.19	16.44	7.97	7.25	17.19	8.51	9.7
YPM 1800	288	118	17	52	83	36	28	69	38	39
YPM 1800	291	116	18	51	85	30	32	63	39	40
CM 3392	194	66.96	21.24	14.16	49.39	20.76	18.87	48.18	16.54	15.92
CM 9900	291	116.05	23.91	32.52	87.2	27.89	25.62	58.22	34.72	29.94
CM 21786	178	57.5	13.49	20.83	41.1	17.47	15.3	34.31	20.52	18.52
CM 30745	275	147.26	14.44	46.16	65.29	35.37	31.2	61.65	34.38	41.6
CM 1066	634	310	32.02	72.87	164	64.93	79.63	140.82	77.5	90.84
CM3392/21786	187.69	71.27	16.03	28.07	56.89	19.59	20.02	42.42	24.46	25.84
CM3392/21786	188.4	70.64	13.04	32.2	57.57	20.78	17.94	44.34	24.52	24.77
BMNH R192	145.17	52.76	9.84	15.15	38.47	16.23	12.38	30.03	16.47	17.61
BMNH R194	105.93	34.3	5.32	10.32	26.47	10.76	9.55	19.2	14.75	12.05
BMNH R196	105.41	37.46	7.14	12.67	28.17	11.41	8.57	23.58	8.73	13.44
BMNH R196	105.38	39.68	5.62	26.76	16.27	10.22	11.07	23.09	16.3	15.33
BMNH R5830	74.56	25.03	3.34	8.79	17.81	5.34	7.01	13.09	8.73	8.5
BMNH RU B.17	65.84	21.93	3.63	6.4	19.24	6.8	6.86	15.19	7.88	5.25
BMNH R3640	602	299	42.81	87.54	174	81.63	71.14	135.86	79.17	99.17
CM 11337	223	90.26	12.56	32.15	69.57	25.66	22.2	50.69	28.08	28.52
CM 11337	224	88.71	16.67	33.94	68.39	27.45	23.17	49.72	27.43	28.25
CM 9185	157.67	69.43	3.79	20.27	45.94	20.08	15.05	46.98	16.5	18.81
CM 9461	414	211	19.91	51.23	123.65	50.03	57.5	103.5	60.54	60.49

Table 2. Measurements used in the traditional morphometric analysis of the scapula. Abbreviations described in Table 3.2

ID#	SL	SAW	BL	MBW	SSL	SCAL	PBW	SAL	IAL
MOR1636	154.11	82.42	115.9	30.81	60.12	70.38	88.32	108.67	129.04
MOR1636	142.32	87.06	105.39	30.4	62.73	73.78	93.18	102.13	120.2
MOR 1642	145.82	77.11	99.99	29.38	59.02	56.66	80.31	99.87	120.94
MOR 294	66.17	28.51	54.46	10.64	23.56	21.44	26	55.99	59.13
MOR 623	93.14	43.48	60.79	14.73	33.13	33.61	38.61	69.86	75.68
MOR 547 W-25-2	365	52	240	38	88	48	84	361	330
BYU 631-163	87.81	48.51	67.54	14.15	40.8	38.26	44.09	86.37	83.24
BYU 17948	292	91.32	230	44.51	62.71	64.4	83.08	280	283
BYU 17945	324	105.55	251	52.57	65.12	83.45	128.98	278	294
BYU 12192	1020	280	830	140	215	150	230	1030	970
DBDP-185	314	96.87	244	47.25	64.11	81.32	89.08	287	280
UMNH VP20644	171	82.13	132.02	35.27	54.22	60.22	115.34	150.47	154.1
UMNH VP20208	455	139.75	361	60.99	84.76	87.66	131.61	419	409
UMNH VP16567	502	183	391	85.62	104.26	92.74	184	446	455
MOR 584	204	59.72	151.68	26.76	47.76	28.87	58.49	205	188
MOR 584	218	58.65	171	25.83	50.23	29.02	58.65	214	205
MOR 584	173	52.52	126.74	21.69	40.88	26.7	57.08	173	153
MOR 682	319	129.25	262	60.71	100.97	108.24	127.54	290	273
MOR 1071	767	170	595	115.02	250	102.07	185	732	694
YPM 6794	291	138.68	223	53.98	67.72	105.83	83.92	258	277
YPM 8611	483	169	397	70.44	77.12	135.75	178	433	466
YPM 1877	435	155	339	75.11	100.83	128.11	165	378	416
YPM 56454	208	71.71	162	29.13	46.58	61.99	65.08	191	187
YPM 5456	526	134.02	367	92.51	134.72	92.82	179	460	420
YPM 4546	508	162	398	95.94	105.48	97.34	179	448	409
YPM-PU 22503	764	169	592	112.86	245	96.91	188	706	658
YPM 1800	387	125	314	55	78	70	140	350	340
YPM 1800	388	130	317	54	76	73	134	355	334
CM3392/21786	178.16	55.32	149.54	31.44	40.08	34.34	81.43	153.37	161.95
CM3392/21786	178.77	51.98	151.41	27.37	34.88	36.02	72.23	159.18	169.3
BMNH R192	134.38	53.81	109.97	21.98	42.32	30.2	49.86	135.28	128.8
BMNH R196	93.96	39.33	77.81	14.82	33.62	34.74	45.66	77.25	82.41
BMNH R196	91.34	40.99	69.76	15.03	30.49	31.94	46.14	68.35	71.87
BMNH RU B.17	72.15	12.53	60.72	9.37	12.28	11.46	23.07	65.57	64.73
BMNH R11000	162	74.3	130	19.79	63.03	56.36	64.06	151	157
BMNH R2519	629	212	466	103.5	120	136.72	121.98	608	565

BMNH R2196	546	160	449	64.22	97	67.64	82.03	540	520
BMNH R2848	933	347	718	139.7		181	286	859	803
BMNH R966	857	344	643	134.95	221	201	242	816	758
BMNH R4743	740	236	635	113.37	84	198	144.26	710	660
CM 11337	310	102.05	231	45.17	85.14	64.09	100.99	280	279
CM 11337	297	102.09	224	44.3	84.71	53.15	105.98	270	269
CM 9185	179.47	56.62	138.88	23.34	49.11	33.97	49.94	178.28	181.2
CM 9461	567	144.49	434	80.56	149.74	76.94	151.6	579	536

Table 3. Measurements used in the traditional morphometric analysis of the coracoid. Abbreviations described in Table 3.3

ID#	CL	CH	CMH	CIW	SPH	CFPe	CFPa	SCAL
MOR 1636	58.77	82.54	68.87	21.83	16.27	14.34	23.36	70.45
MOR 1642	63.19	70.78	60.27	26.57	15.75	11	12.99	52.14
MOR 623	45.57	53.73	41.44	24.8	8.37	10.44	12.25	33.92
BYU 631-163	40.69	48.65	35.2	18.3	8.03	11.25	6.67	38.26
UMNH VP16422	100.9	134.8	116	47.93	13.37	9.33	10.81	62.29
YPM 1877	118.9	140.3	116.1	37.09	28.3	16	6.13	88.61
YPM 5478	42.85	49.56	41.69	17.69	8.9	10.35	6.23	31.66
YPM 5456	170	135.5	117.9	74.47	40.76	48.19	23.17	92.85
YPM 1800	116	107	82	40	17	15	4	66
YPM 1800	102	122	106	41	19	11	4	79
CM3392/21786	48.68	52.21	41.11	24.13	7.47	3.75	11.57	36.02
CM3392/21786	52.88	53.11	44.79	27.03	16.04	4.3	9.4	38.4
BMNH R192	39.35	54.36	37.97	22.81	13.51	5.8	10.36	27.34
BMNH R196	29.94	42.65	35.99	19.85	9.84	9.42	3.14	31.2
BMNH R196	32.83	43.21	35.01	16.93	6.93	8.78	6.09	31.94
BMNH R11000	48.11	70.36	59.96	24.89	4.38	11.15	7.99	57.79
CM 11337	67.77	87.17	66.95	34.23	23.57	11.99	1.82	58.19
CM 11337	65.88	84.74	69.75	30.56	18.36	12.98	3.44	58.28
CM 9185	59.16	53.54	52.62	28.25	22.01	14.55	0.01	32.46
CM 9461	120.3	97.45	71.7	41.95	30.14	35.74	12.69	69.38

APPENDIX D

LOADINGS AND IMPORTANCE OF AXES OF ANALYSES

PCA standard deviations and loadings

Humerus

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Importance of components:
                          Comp.1    Comp.2    Comp.3     Comp.4     Comp.5
Standard deviation     1.8480650 1.3221990 1.1147638 0.90684505 0.71443994
Proportion of Variance 0.3794827 0.1942456 0.1380776 0.09137422 0.05671382
Cumulative Proportion  0.3794827 0.5737283 0.7118059 0.80318007 0.85989389
                           Comp.6     Comp.7     Comp.8     Comp.9
Standard deviation     0.69475666 0.55582956 0.50342707 0.46463195
Proportion of Variance 0.05363187 0.03432739 0.02815987 0.02398698
Cumulative Proportion  0.91352576 0.94785315 0.97601302 1.00000000
```

Loadings:

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5	Comp.6	Comp.7	Comp.8	Comp.9
DL	-0.287	0.113	0.602	-0.339	0.117	0.376	-0.383	-0.335	0.116
DW	-0.171	-0.448	-0.237	-0.632	-0.507		0.199		
HHW	-0.290	0.273	-0.471	-0.343	0.510	-0.295		-0.247	0.304
HPW	-0.345	-0.396	-0.110	0.419	-0.207	-0.205	-0.469		0.477
HSW	-0.397	-0.266	0.179	0.327	0.226	0.216	0.696	-0.202	
HSP	-0.338	0.214	0.420		-0.270	-0.726	0.160		-0.179
HDW	-0.408	-0.351			0.382		-0.262	0.338	-0.609
RCW	-0.309	0.399	-0.355	0.277	-0.354	0.228		-0.431	-0.415
UCW	-0.391	0.395			-0.173	0.308		0.688	0.285

Scapula

```
Importance of components:
                           Comp.1    Comp.2    Comp.3     Comp.4     Comp.5
Standard deviation     2.1632044 1.1102922 0.9640055 0.60237754 0.57260515
Proportion of Variance 0.5849316 0.1540936 0.1161633 0.04535734 0.04098458
Cumulative Proportion  0.5849316 0.7390252 0.8551886 0.90054590 0.94153049
                           Comp.6    Comp.7     Comp.8
Standard deviation     0.50361341 0.3659082 0.28326816
Proportion of Variance 0.03170331 0.0167361 0.01003011
Cumulative Proportion  0.97323379 0.9899699 1.00000000
```

Loadings:

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5	Comp.6	Comp.7	Comp.8
SAW	0.406	0.279	0.163	0.147		0.491	0.232	0.644
BL	-0.130	0.701	-0.510		-0.450	-0.135		
MBL	0.375		-0.305	-0.796	0.122	0.193	-0.283	
SSL	0.345		0.547		-0.612	-0.301	-0.324	
SCAL	0.414	0.254		0.308		0.364		-0.721
PBW	0.416	0.163		-0.133	0.189	-0.583	0.633	
SAL	-0.390	0.129	0.318	-0.445	-0.315	0.341	0.513	-0.231
IAL	-0.250	0.568	0.460	-0.144	0.516	-0.158	-0.298	

Coracoid

```
Importance of components:
                           Comp.1    Comp.2    Comp.3    Comp.4     Comp.5
Standard deviation     1.7171238 1.1445457 1.0006791 0.9021004 0.83222205
```

```
Proportion of Variance 0.4212163 0.1871407 0.1430512 0.1162550 0.09894193
Cumulative Proportion  0.4212163 0.6083570 0.7514082 0.8676633 0.96660519
                          Comp.6      Comp.7
Standard deviation     0.40468630 0.264561263
Proportion of Variance 0.02339586 0.009998952
Cumulative Proportion  0.99000105 1.000000000
```

Loadings:

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5	Comp.6	Comp.7
CH	-0.543	0.212	0.126			-0.263	0.754
CMH	-0.518	0.221	0.211	0.133	-0.203	-0.413	-0.639
CIW	-0.318	-0.287	0.366		0.808	0.136	
CHH		-0.587	0.554	-0.228	-0.520	0.145	
CFPe		-0.653	-0.378	0.560		-0.326	
CFPa	-0.256	-0.227	-0.512	-0.760		-0.195	
SCAL	-0.509		-0.306	0.184	-0.174	0.760	

RWA Loadings

Humerus

Consensus configuration after sliding (Describes the "average" shape):

1	0.287624	-0.192559
2	0.400222	-0.031373
3	0.137362	0.027894
4	-0.246134	0.119551
5	-0.293610	0.089972
6	-0.288921	0.045601
7	-0.311264	0.002163
8	-0.276706	-0.041737
9	0.205994	-0.122661
10	0.122669	-0.065998
11	0.040472	-0.037617
12	-0.057190	-0.024302
13	-0.168101	-0.032653
14	0.286176	0.016658
15	0.181040	0.055731
16	0.102453	0.062432
17	0.001720	0.053338
18	-0.123805	0.075559

Singular values and percent explained for relative warps:

No.	SV	%	Cum %
1	0.65830	60.27%	60.27%
2	0.34692	16.74%	77.01%
3	0.19964	5.54%	82.55%
4	0.17163	4.10%	86.65%
5	0.15701	3.43%	90.07%
6	0.15298	3.25%	93.33%
7	0.10469	1.52%	94.85%
8	0.10003	1.39%	96.24%
9	0.08253	0.95%	97.19%
10	0.07066	0.69%	97.89%
11	0.05449	0.41%	98.30%
12	0.04831	0.32%	98.62%
13	0.04469	0.28%	98.90%
14	0.04236	0.25%	99.15%
15	0.03678	0.19%	99.34%
16	0.03254	0.15%	99.49%
17	0.03045	0.13%	99.62%

18	0.02860	0.11%	99.73%
19	0.02280	0.07%	99.80%
20	0.02088	0.06%	99.86%
21	0.01882	0.05%	99.91%
22	0.01685	0.04%	99.95%
23	0.01413	0.03%	99.98%
24	0.00852	0.01%	99.99%
25	0.00599	0.00%	99.99%
26	0.00372	0.00%	100.00%
27	0.00364	0.00%	100.00%
28	0.00282	0.00%	100.00%
29	0.00241	0.00%	100.00%
30	0.00157	0.00%	100.00%
31	0.00108	0.00%	100.00%
32	0.00069	0.00%	100.00%

Scapula

Consensus configuration after sliding:

1	0.283706	0.054629
2	0.279826	0.075496
3	0.256930	0.083087
4	-0.193622	0.071647
5	-0.221323	-0.120204
6	0.214039	-0.095029
7	0.257239	-0.051831
8	0.171148	0.003487
9	0.212053	0.060960
10	0.129910	0.057738
11	0.040214	0.062977
12	-0.053787	0.065702
13	-0.132500	0.068283
14	-0.215546	0.055292
15	-0.237432	0.028444
16	-0.255873	-0.008012
17	-0.262301	-0.051146
18	-0.247384	-0.099385
19	-0.162256	-0.087398
20	-0.093496	-0.058875
21	-0.007525	-0.038902
22	0.081606	-0.031581
23	0.156375	-0.045379

Singular values and percent explained for relative warps:

No.	SV	%	Cum %
1	0.64201	58.54%	58.54%
2	0.30615	13.31%	71.85%
3	0.24802	8.74%	80.59%
4	0.20005	5.68%	86.27%
5	0.17885	4.54%	90.82%
6	0.13809	2.71%	93.52%
7	0.10059	1.44%	94.96%
8	0.08334	0.99%	95.95%
9	0.07675	0.84%	96.78%
10	0.06761	0.65%	97.43%
11	0.06270	0.56%	97.99%
12	0.05072	0.37%	98.36%
13	0.04835	0.33%	98.69%
14	0.04599	0.30%	98.99%
15	0.04184	0.25%	99.24%
16	0.04035	0.23%	99.47%
17	0.03029	0.13%	99.60%
18	0.02702	0.10%	99.70%
19	0.02269	0.07%	99.78%
20	0.02106	0.06%	99.84%
21	0.01877	0.05%	99.89%
22	0.01491	0.03%	99.92%
23	0.01224	0.02%	99.94%
24	0.01116	0.02%	99.96%
25	0.00959	0.01%	99.97%
26	0.00800	0.01%	99.98%
27	0.00644	0.01%	99.99%
28	0.00531	0.00%	99.99%
29	0.00457	0.00%	99.99%
30	0.00414	0.00%	100.00%
31	0.00305	0.00%	100.00%
32	0.00235	0.00%	100.00%
33	0.00205	0.00%	100.00%
34	0.00146	0.00%	100.00%
35	0.00136	0.00%	100.00%
36	0.00068	0.00%	100.00%

Coracoid

Consensus configuration after sliding:

1	0.334991	0.143209
2	-0.038385	0.282977
3	-0.233866	0.184800

4	-0.177899	0.104923
5	-0.199794	0.029249
6	-0.312083	-0.074847
7	0.052182	0.118065
8	0.006997	0.130200
9	0.326722	0.022418
10	0.282996	-0.104717
11	0.196284	-0.203120
12	0.069278	-0.234118
13	-0.080069	-0.225702
14	-0.227354	-0.173338

Singular values and percent explained for relative warps:

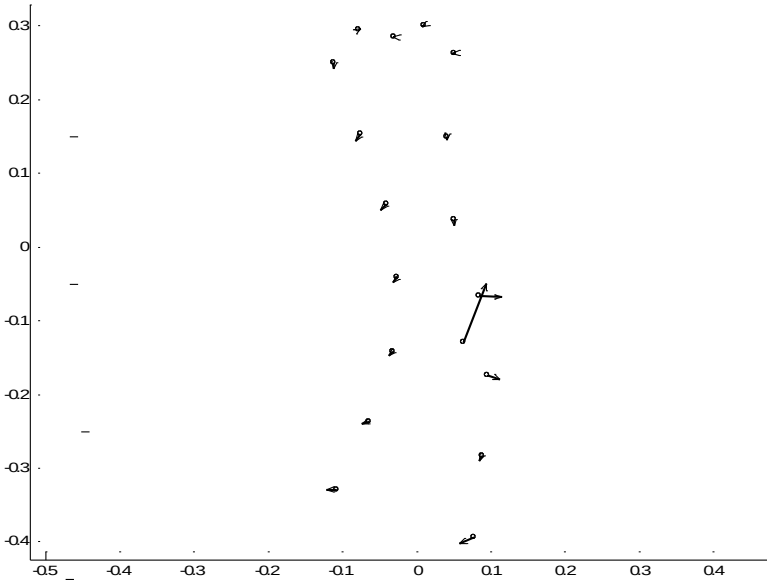
No.	SV	%	Cum %
1	0.38726	38.18%	38.18%
2	0.27526	19.29%	57.46%
3	0.21523	11.79%	69.26%
4	0.20162	10.35%	79.60%
5	0.16263	6.73%	86.34%
6	0.12445	3.94%	90.28%
7	0.12193	3.78%	94.06%
8	0.09555	2.32%	96.39%
9	0.07272	1.35%	97.73%
10	0.05861	0.87%	98.61%
11	0.04864	0.60%	99.21%
12	0.03426	0.30%	99.51%
13	0.02829	0.20%	99.71%
14	0.02491	0.16%	99.87%
15	0.01751	0.08%	99.95%
16	0.01032	0.03%	99.98%
17	0.00897	0.02%	100.00%
18	0.00398	0.00%	100.00%

CVA Loadings

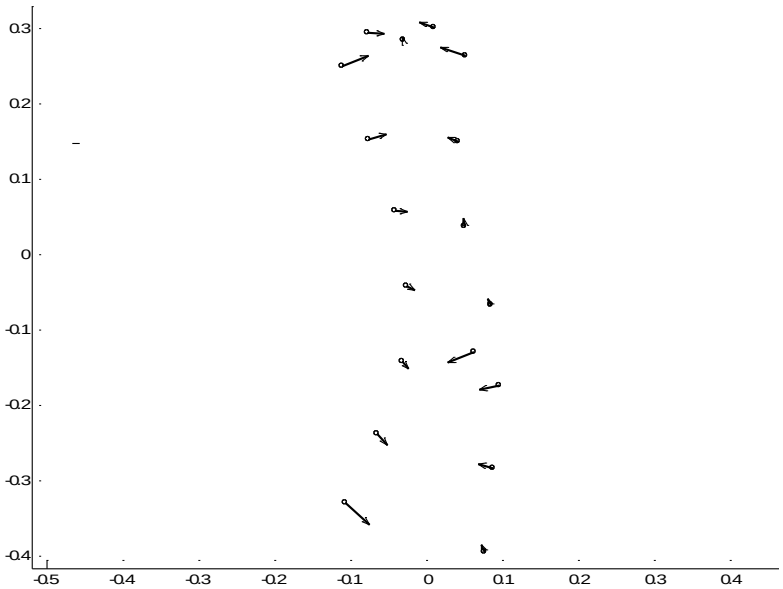
Humerus

Results from CVA/Manova
Axis 1 Lambda= 0.0001 chisq=334.1398 df=192 p=9.14993e-010
Axis 2 Lambda= 0.0024 chisq=226.6755 df=155 p=0.000153791
Axis 3 Lambda= 0.0149 chisq=157.7605 df=120 p=0.011836

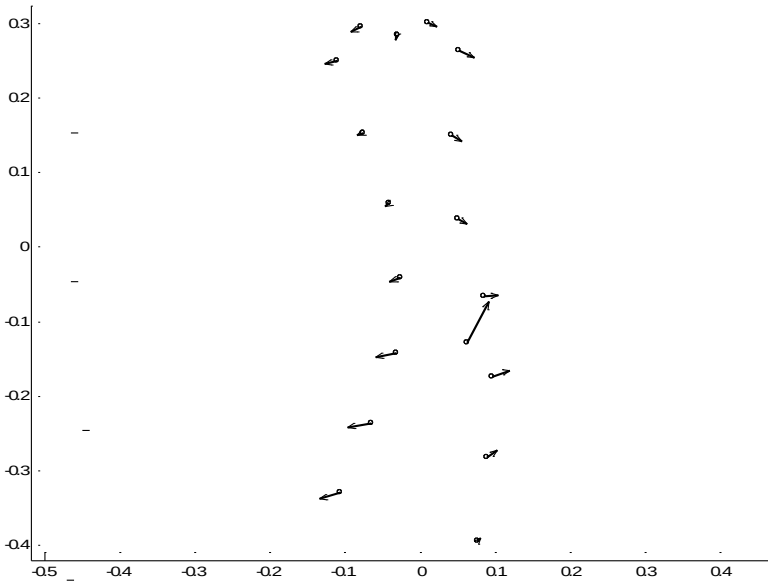
Axis 1 Deformation (Procrustes):



Axis 2 Deformation (Procrustes):



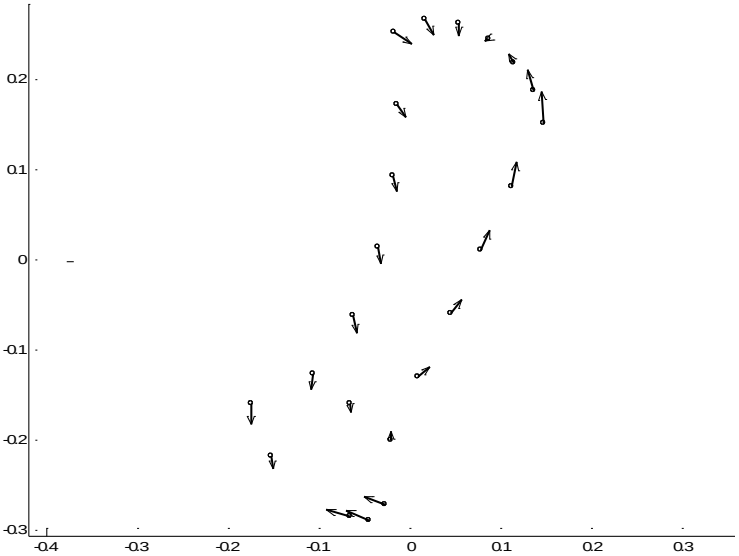
Axis 3 deformation (Procrustes):



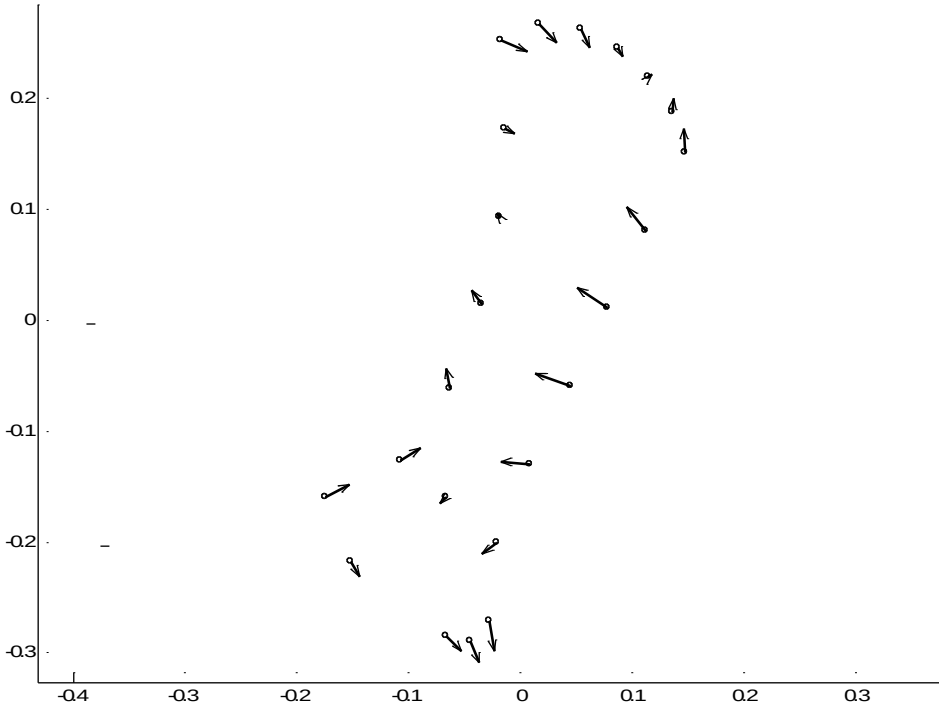
Scapula

Results from CVA/Manova (On 7 PCs):
Axis 1 Lambda= 0.0083 chisq=139.0790 df=30 p=5.55112e-016
Axis 2 Lambda= 0.0927 chisq=68.9829 df=20 p=2.66727e-007
Axis 3 Lambda= 0.3587 chisq=29.7350 df=12 p=0.00306057
Axis 4 Lambda= 0.6200 chisq=13.8623 df=6 p=0.0312123

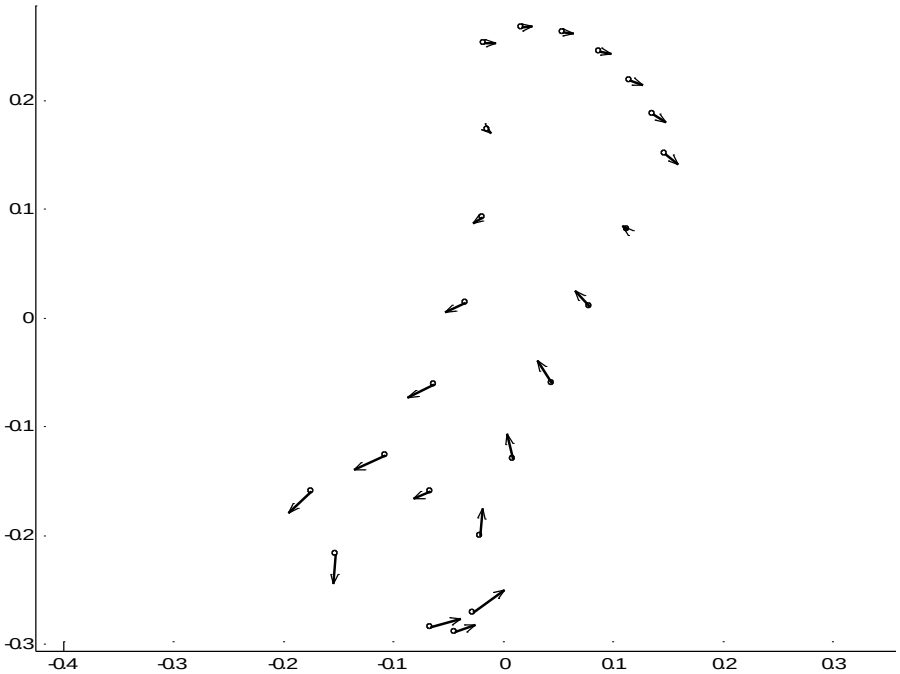
Axis 1 deformation (Procrustes):



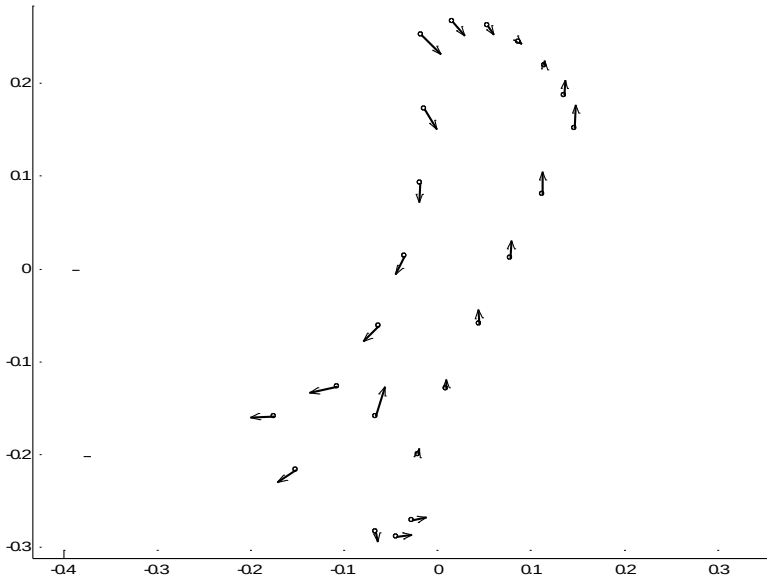
Axis 2 deformation (Procrustes):



Axis 3 deformation (Procrustes):



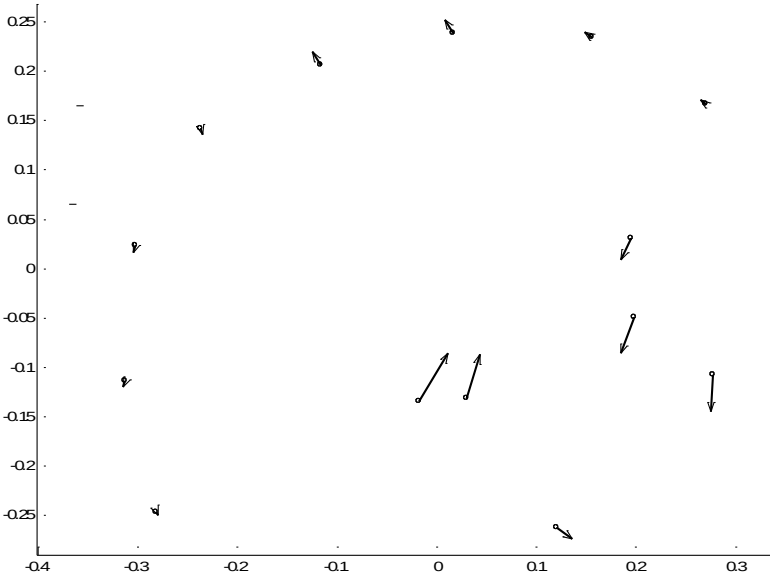
Axis 4 deformation (Procrustes):



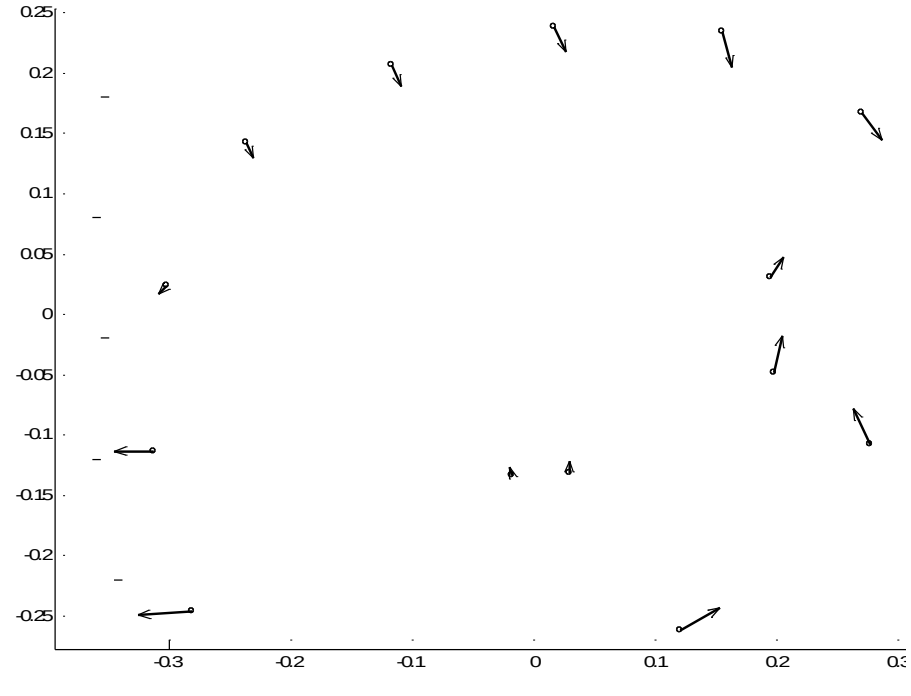
Coracoid

Results from CVA/Manova
Axis 1 Lambda= 0.0257 chisq=47.6194 df=20 p=0.000480928
Axis 2 Lambda= 0.1115 chisq=28.5187 df=12 p=0.00464201
Axis 3 Lambda= 0.3429 chisq=13.9155 df=6 p=0.0305945

Axis 1 deformation (Procrustes):



Axis 2 Deformation (Procrustes):



Axis 3 Deformation (Procrustes):