

**FURTHER DESCRIPTIONS OF THE OSTEOLOGY OF *DEINONYCHUS ANTIRRHOPUS*
(SAURISCHIA, THEROPODA)**

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ABSTRACT - Developmental and/or functional implications are described for aspects of *Deinonychus antirrhopus* scapula, pedal, and long bone morphology. Differences in claw curvature are identified as indicators of juvenile development, and the presence of periosteal rest lines as evidence for determinate growth is confirmed. The asymmetric ventral keel morphology that is characteristic of certain tree-climbing birds is also documented for the penultimate phalanx of the second pedal digit. The lateral orientation of the scapula glenoid and the presence of a scapulohumeral ligament would allow the forelimb an arc of movement that would reach angles extensively above and below the horizontal plane. Like *Archaeopteryx*, *Deinonychus* has a robust deltopectoral crest anchoring a robust pectoralis muscle. Proximal lateral flanges are present on the first phalanx of second manual digit. These features provide additional evidence concerning the behavioral morphology of *Deinonychus* and some other members of Dromaeosauridae.

INTRODUCTION

Since publication of Ostrom's (1969) description of *Deinonychus antirrhopus*, certain features or the morphology of single dromaeosaurid bones have played a significant role in speculations regarding the origin of flight, terrestrial and/or arboreal behavior, possible endothermy, and the evolutionary relationship between dromaeosaurids and birds. Examples of these significant singular skeletal elements or features are the semi-lunate carpal of *Deinonychus* (Ostrom, 1969) with respect to the evolution of avian forelimb movement, feather quill knobs on the ulna of *Velociraptor mongoliensis* as evidence of aerodynamic flight feathers on dromaeosaurids (Turner et al, 2007), the morphology and function of the second pedal ungual as evidence of arboreal behavior (Manning et al., 2006), and the posterolateral flanges on the proximal phalanx of the second manual digit as evidence of aerodynamic flight feathers on the forelimbs of some members of Dromaeosauridae (Paul, 2002).

Adding to the list of important dromaeosaurid skeletal elements, we will describe the functional significance of the ventral keel on penultimate phalanx of the second pedal ungual, the morphology of the proximal end of the scap-

ula (including the orientation of the glenoid and the presence of a robust scapulohumeral ligament fossa), and the histology of the radius. Our analysis of the penultimate phalanx of the second pedal ungual and morphology of the second pedal ungual compliments research on the arboreal behavior of certain members of Dromaeosauridae by Manning et al. (2006).

Our histological analysis of the radius and in particular the discovery of the presence of periosteal rest lines represents a continuation of our previous research on this aspect of the limb bones of *Deinonychus* (Parsons and Parsons, 2006) as well as observations made by Ostrom (1969). Our analysis of the scapula, the scapular glenoid, and the shoulder joint of *Deinonychus* and the functional implications of this newly discovered skeletal feature expands upon the interpretations of the forelimb movement and function of *Deinonychus* and/or other dromaeosaurids presented by Baier et al. (2007), Senter (2006a and 2006b), and Gishlick (2001).

MATERIAL AND METHODS

Specimens - Specimens were chosen from collections of the American Museum of Natural History, the Yale/ Peabody Museum of Natural History, the Mongolian Institute of Geology, the

Museum of the Rockies, The Buffalo Museum of Science, The Royal Ontario Museum, and the Museum of Comparative Zoology. Several articulated and unarticulated theropod skeletons were examined and compared with two newly discovered specimens of *Deinonychus* (MOR 1178, MOR 1182). Museum specimens of *Deinonychus* included AMNH 3015, MCZ 8791, MCZ 4371, YPM 5205, and YPM 5206. Other theropod specimens examined were *Ornitholestes hermanni*, AMNH 619; *Bambiraptor feinbergi*, FR 30556; *Albertosaurus libratus*, ROM 762; and the *Velociraptor mongoliensis* specimens IGM 100/982, 100/985, and 100/986.

Extant mammalian and avian skeletons were examined within the zoological collections of the Buffalo Museum of Science in Buffalo, New York, and the Royal Ontario Museum in Toronto, Ontario. Some of the BMS and ROM specimens are presented in Figures 1 and 2.

Photographs were made of IGM *Velociraptor* specimens and the MCZ and YPM *Deinonychus* specimens (Fig. 1, 2, 4, 6, 8, 9, 10). The graphings of the morphological outlines of the second pedal unguals of YPM 5205, IGM 100/982, and IGM 100/985 were created using measurements from the actual specimens and photographs upon a gridded background (Fig. 3). The curvature outline of second pedal ungual of MCZ 4371 was taken from the text of Ostrom (1976).

Measurement of angles - Orientations of various theropod scapular glenoids were made by placing the various scapula specimens a sand box for support. The angles between the plane of the floor of the glenoid on the scapula/coracoids to the plane of the lateral surface of the scapular blade were created by placing a small metric ruler parallel to the plane of the widest dorso/ventral measure of the floor of the glenoid and another metric ruler along the shaft of the scapular blade at the proximal-most point closest to the glenoid. The ruler placed along the shaft of the blade was set parallel to the plane of the widest dorso/ventral measure of the blade of the scapula and at the proximal-most point from which the plane of the blade of the scapula could be determined. These rulers extended well beyond the limit of either scapular surface. With

the camera directed proximally, from a position distally aligned with the surface of the plane of the blade of the scapula, these two metric rulers were photographed as they each extended beyond the long axis of the blade of the scapula. The positioning of the camera as level with the long axis of the blade of the scapula brought both rulers into alignment such that an angle was created that represented the difference in the orientation between those two planes.

Histological sections - Two thin sections were removed from very small *Deinonychus* bone fragments. The taphonomic processes that affected the fossils at these two new *Deinonychus* sites resulted in the creation of numerous small fragments of bone. Initially, much of the more fragmented material seemed of somewhat less value than the more complete skeletal elements, but on further examination, it became apparent that when both the diameter of a limb bone fragment and the ratio of the diameter of a limb bone fragment to the diameter of the medullary cavity were compared even fairly small limb bone fragments could be accurately identified. Using this method, we created thin sections from two small fragments of radii while not destroying any of the more intact skeletal elements.

Institutional Abbreviations - **AMNH**, American Museum of Natural History; **BMS**, Buffalo Museum of Science; **IGM**, Mongolian Institute of Geology; **MCZ**, Museum of Comparative Zoology; **MOR**, Museum of the Rockies; **ROM**, Royal Ontario Museum; **YPM**, Yale/Peabody Museum of Natural History.

DESCRIPTION

The following descriptions provide information missing from the initial osteological documentation of *Deinonychus* made by Ostrom (1969, 1974, 1976).

Penultimate phalanx on second pedal digit

The ventral surface of this phalanx (Fig. 1 A1–A3) possesses a keel-like ventral extension asymmetrically positioned in relation to the long axis of the phalanx. A similar ventral keel is present on the proximal pedal III–2 phalanx of *Dryocopus pileatus* (ROM 96677, pileated woodpecker) (Fig. 1B) and on the same phalanx of *Melanerpes erythrocephalus* (BMS 9141, redheaded woodpecker) (Fig. 1C).

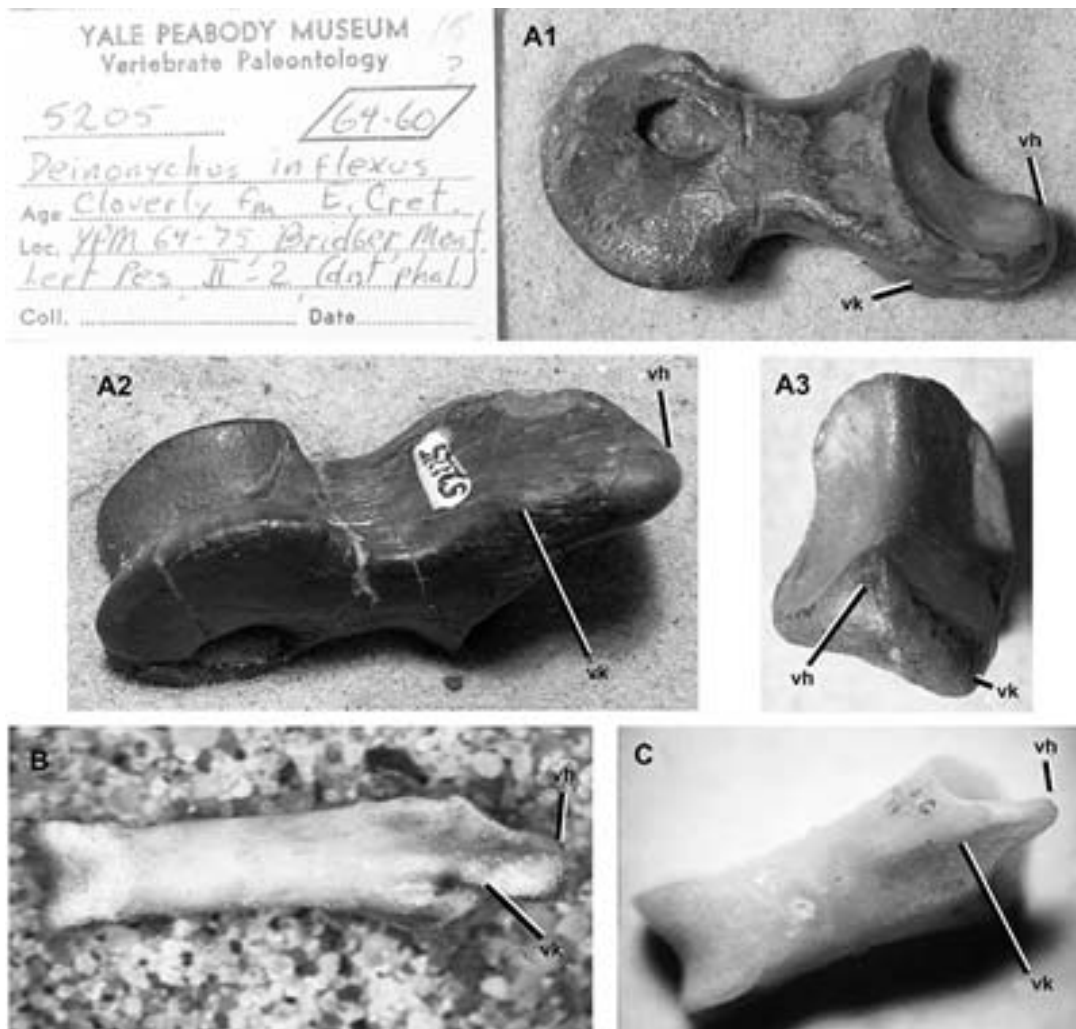


Figure 1. (A1) Lateral view of YPM 5205 left pedal II-2 phalanx. (A2) Ventral view of YPM 5205 left pedal II-2 phalanx. (A3) Caudal view of YPM 5205 left pedal II-2 phalanx.; (B) Proximal pedal III-2 phalanx of *Dryocopus pileatus* (ROM 96677, pileated woodpecker); (C) Proximal pedal III-2 phalanx of *Melanerpes erythrocephalus* (BMS 9141, redheaded woodpecker). **Abbreviations:** vh, ventral heel; vk, ventral keel. Copyright of images of YPM specimens held by Yale Peabody Museum. Copyright of images of BMS specimens held by Buffalo Museum of Science. Copyright of images of ROM specimens held by Royal Ontario Museum.

Second pedal ungula - The inner claw arc of the pedal digit II of *Deinonychus* is 160° (Manning et al., 2006). There is a greater similarity between the inner arc curvatures of the pedal unguals of *Melanerpes* (Fig. 2B) and the second pedal ungual of *Deinonychus* (Fig. 2A) than between the second pedal unguals of *Deinonychus* and *Velociraptor* (Fig. 2C). Lateral compression of this *Deinonychus* ungual is also more

similar to that of *Melanerpes* than that of *Velociraptor* (Fig. 2).

Cross-sectional thicknesses of long bones midshafts - From visual comparisons of the ratios of bone matrix thickness to medullar cavity thickness within various long bone cross sections, it became apparent that the radius possessed the smallest medullar cavity compared to the bone matrix (Fig. 4C).

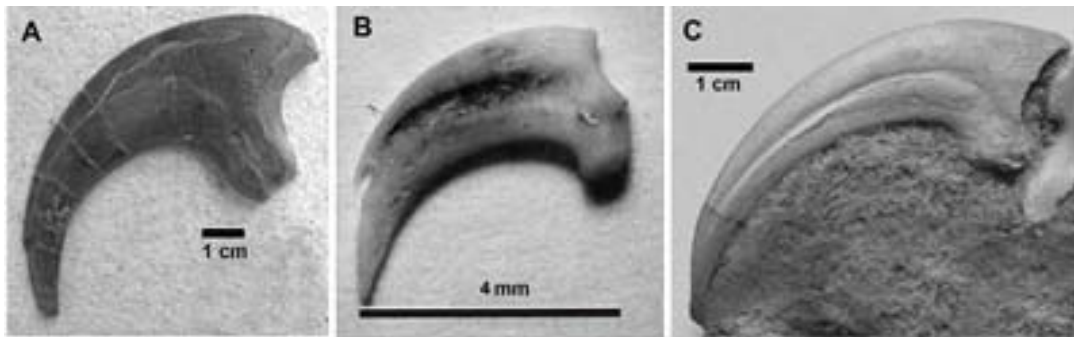


Figure 2. (A) *Deinonychus* YPM 5205 second pedal ungual. (B) *Melanerpes erythrocephalus* (BMS 9141, redheaded woodpecker) second pedal ungual. (C) *Velociraptor* IGM 100/985 second pedal ungual. Note that the lateral compression and inner arc curvature on the unguals of *Deinonychus* and *Melanerpes* are more similar than the morphologies of the *Deinonychus* ungual compared to the second pedal ungual of *Velociraptor*. Copyright of images of YPM specimens held by Yale Peabody Museum. Copyright of images of BMS specimens held by Buffalo Museum of Science. Copyright of images of IGM specimens held by Mongolian Institute of Geology.

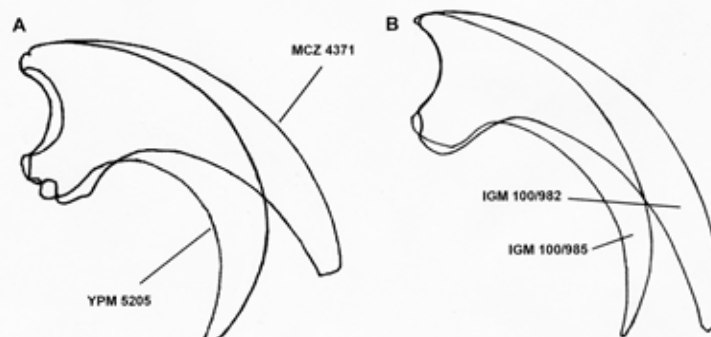


Figure 3. (A) Comparison of the inner arc curvature on the second pedal unguals on *Deinonychus* specimen MCZ 4371 and *Deinonychus* specimen YPM 5205. (B) Comparison of the inner arc curvatures on the second pedal unguals on *Velociraptor* specimens IGM 100/982 (adult) and IGM 100/985 (sub-adult). Copyright of images of YPM specimens held by Yale Peabody Museum. Copyright of images of MCZ specimens held by Museum of Comparative Zoology, Harvard University. Copyright of images of IGM specimens held by Mongolian Institute of Geology.

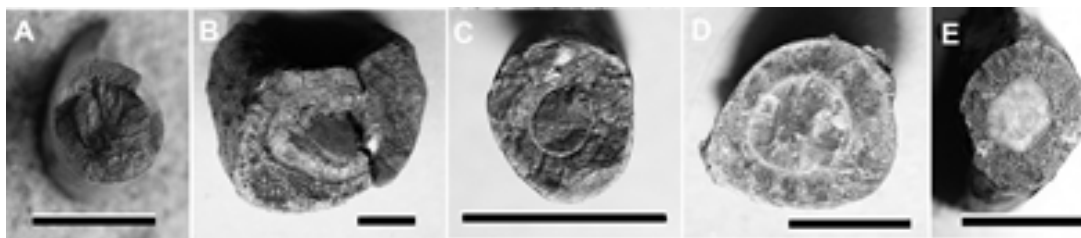


Figure 4. Five cross sections of major limb bones of *Deinonychus*. (A) Ulna, MCZ 8791 (juvenile). (B) Femur, MOR 1178. (C) Radius, MOR 1178. (D) Humerus, MOR 1178. (E) Fibula, MOR 1178. (F) Tibia, MOR 1178. Scale bars are all equal to 1 cm. Copyright of images of MCZ specimens held by Museum of Comparative Zoology, Harvard University. Copyright of images of MOR specimens held by Museum of the Rockies.

Periosteal rest lines - As was previously reported by Parsons and Parsons (2006), thin sections of fragments of the radii of *Deinonychus* (MOR 1178, Fig. 5A; MOR 1182, Fig. 5B) exhibit periosteal rest lines.

In order to find the most informative limb bone material from which to attempt histological thin section analysis, natural, taphonomic, cross-sectional breakages of all the major limb bones were examined. As to most of the long bones of the forelimbs and hind limbs, within the humerus, ulna, tibia, fibula, and femur, the development of secondary osteon replacement has been so extensive that most of histological data relating to the growth stage processes have been obliterated.

The histology of the radius of the older individual specimen MOR 1182 is almost completely remodeled by secondary osteon replacement, but the radius of the young adult specimen MOR 1178 (physical maturity at 11 to 12 years of age according to LAGs) (Fig. 4C) still possesses a considerable amount of intact histological information such as zonal fibrolamellar tissue, lines of arrested growth, remnants of the more medial LAGs still apparent between secondary osteons, the condensing of lines of arrested growth which is the probable point of sexual maturity, and periosteal rest lines. Cur-

sory examination of the unprepared fragmentary cross section of the radius of *Velociraptor* IGM 100/986 revealed evidence of lines of arrested growth and a small medullar vacuity to that is similar to that found within the radius of *Deinonychus* MOR 1178.

Morphology and orientation of scapular glenoid - The glenoid is shallow, flattened, and posterolaterally facing. It is widest at the point of contact with the coracoid and is caudally tapered. The very shallow morphology of this glenoid would not even partially encapsulate the articulating head of the humerus. Midway between the rostral and caudal limits of the dorsal edge there is a substantial fossa (Fig. 6A2, slf) that is also found along the dorsal edge of the glenoid of *Bambiraptor* (Fig. 6A1). The fossa invades the dorsal edge of the glenoid and occupies a position within a portion of the otherwise articulating surface of the glenoid. This is the scapular insertion point for a relatively robust scapulohumeral ligament (Jenkins, 1993). This fossa is not present in *Velociraptor*.

On *Deinonychus*, the angle created by projecting the plane of the floor of the scapular glenoid to intersect with the plane of the lateral surface of the proximal end of the blade of the scapula created an angle of 35° (Fig. 6A3).

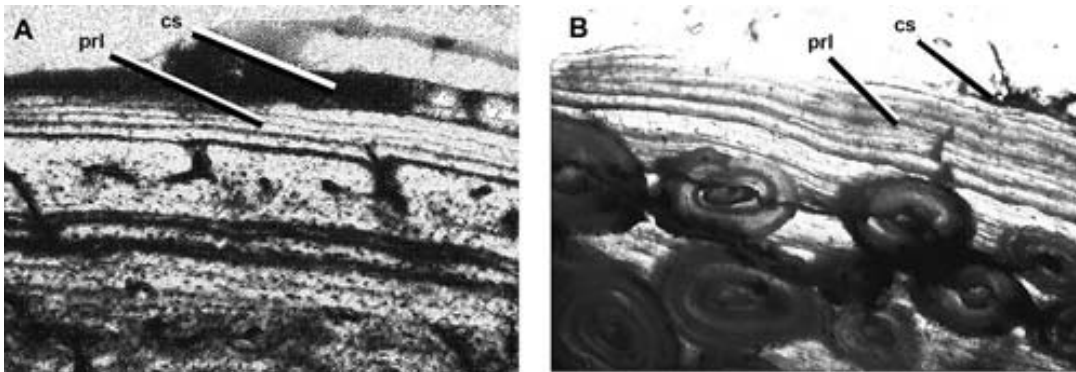


Figure 5. Periosteal rest lines (A) in the radius of *Deinonychus* MOR 1178. (B) and radius of *Deinonychus* MOR 1182. **Abbreviations:** prl, periosteal rest lines; cs, cortical surface. Copyright of images of MOR specimens held by Museum of the Rockies.

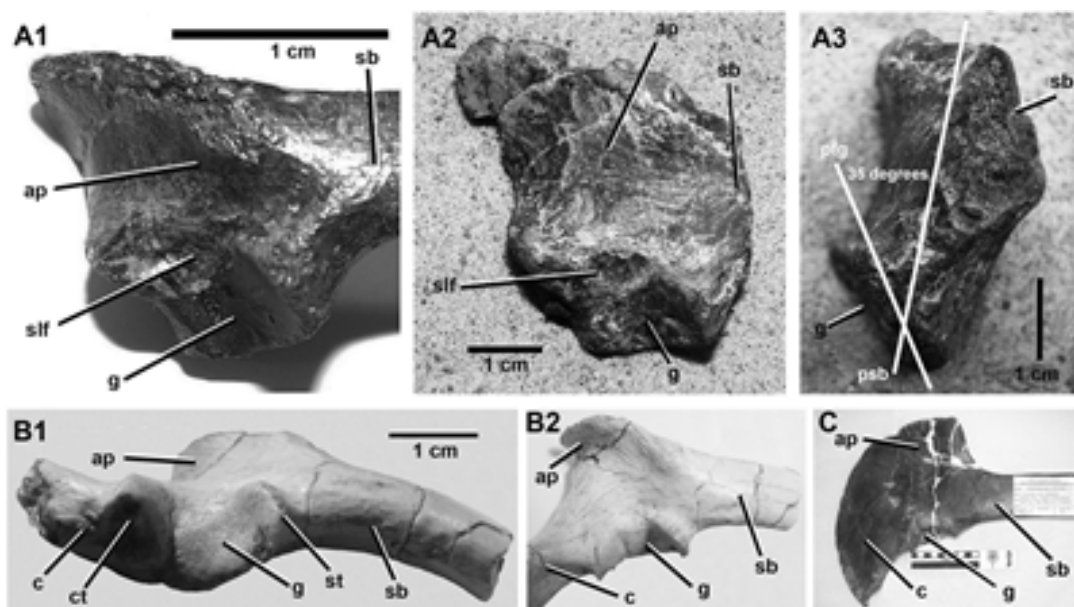


Figure 6. Scapula acromial process and glenoid portion (A1) in *Bambiraptor feinbergi* (FARB 30556, left lateral), (A2) in *Deinonychus* MOR 1178 (left lateral), (A3) in *Deinonychus* MOR 1178 scapula (caudal view); (B1) in *Velociraptor* IGM 100/986 (ventral view), (B2) (left lateral); (C) in *Albertosaurus libratus* ROM 762 (left lateral). **Abbreviations:** ap, acromial process; c, coracoid; ct, coracoidal tuber; dva, dorsoventral axis of the lateral plane of the scapular blade; g, glenoid; pfg, plane of floor of scapular glenoid; psb, plane of the lateral surface of the proximal end of the scapular blade; sb, scapular blade; slf, scapulohumeral ligament insertion fossa; st, scapular tuber. Copyright of images of MOR specimens held by Museum of the Rockies. Copyright of images of ROM specimens held by Royal Ontario Museum. Copyright of images of IGM specimens held by Mongolian Institute of Geology. Copyright of images of AMNH and FARB specimens held by American Museum of Natural History.

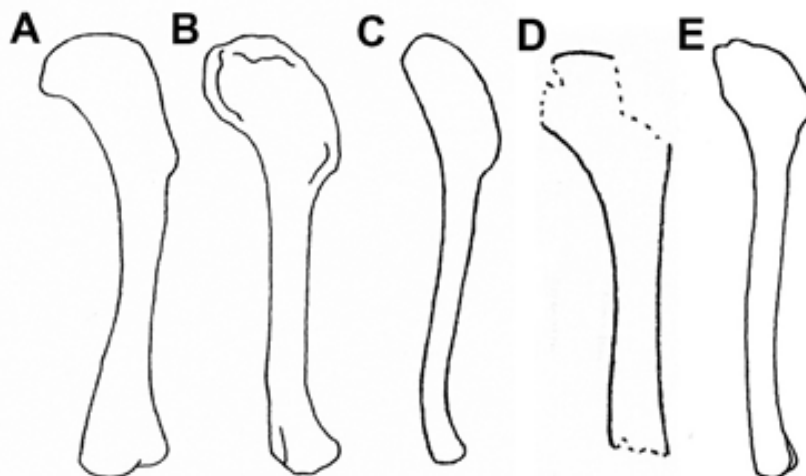


Figure 7. The profiles of five theropod humeri comparing the extent of the development of the deltopectoral crest. (A) *Ornitholestes*, AMNH 619. (B) *Deinonychus*, AMNH 3015. (C) *Archaeopteryx*, holotype, London specimen. (D) *Velociraptor*, IGM 100/985. (E) *Bambiraptor*, FARB 30556. Copyright of images of IGM specimens held by Mongolian Institute of Geology. Copyright of images of AMNH and FARB specimens held by American Museum of Natural History.

Deltopectoral crest on the humerus - The deltopectoral crest on the humerus of *Deinonychus* (Fig. 7B) is more robust than on *Velociraptor* (Fig. 7D) or *Bambiraptor* (Fig. 7E) in that it extends much further distally along the shaft of the humerus. It is similar to the deltopectoral crest of the small theropod *Ornitholestes hermanni*, AMNH 619 (pers. observ.) (Fig. 7A) and *Archaeopteryx lithographica* (Ostrom, 1985; Ostrom et al., 1999) (Fig. 7C).

Proximal lateral flanges on first phalanx of second manual digit - A small, posterolateral flange is preserved on the left side of the left II-1, manual phalanx of *Deinonychus* specimen YPM 5206 (Fig. 8A, plf). This is a fragile process and is only preserved on the left side of this specimen. The flange originally extended in a more laterally horizontal position, but it was taphonomically crushed against the lateral surface of the shaft.

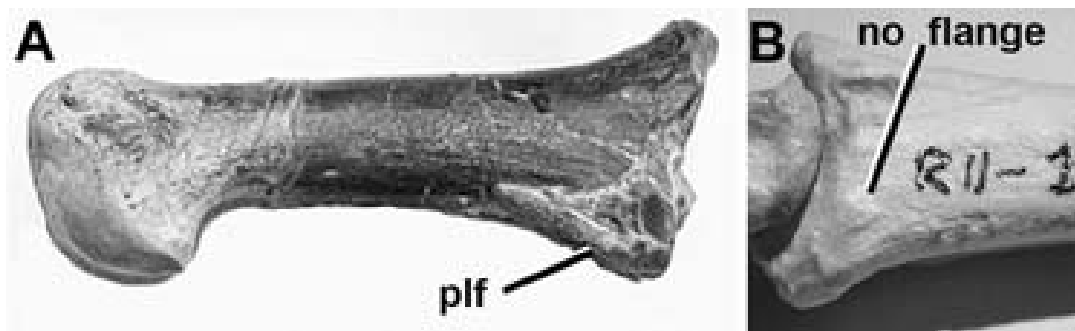


Figure 8. Manual II-1 phalanx, (A) posterolateral flange on left phalanx of *Deinonychus* specimen YPM 5206, (B) right proximal phalanx of *Velociraptor* IGM 100/986. **Abbreviations:** plf, posterolateral flange. Copyright of images of YPM specimens held by Yale Peabody Museum. Copyright of images of IGM specimens held by Mongolian Institute of Geology.

DISCUSSION

The eight skeletal elements/characters reviewed in this study provide additional information on the functional morphology and behavior of *Deinonychus* and other dromaeosaurs, with respect to determinate growth, arboreal activity, differentiation between juvenile and adult life strategies, and more complex forelimb movements than previously hypothesized in the literature.

The ventral keel on the penultimate phalanx on the second pedal digit - Our study of the asymmetric ventral keel and homologous features in some extant avian taxa (Fig. 1) may add further credibility to the contention that *Deinonychus* exhibited arboreal climbing behavior (Manning et al., 2006; Xu and Zhang, 2005). In our observations of many extant avian and mammalian predators that also possess strongly developed curved manual and/or pedal unguals, none exhibited a ventral keel morphology similar to that of *Deinonychus*, but asymmetric ventral keels were observed on the phalanges of *Melanerpes erythrocephalus* (BMS 9141, red-headed woodpecker) (Fig. 1C) and *Dryocopus*

pileatus (ROM 96677, pileated woodpecker) (Fig. 1B).

The presence of this keel on some of the phalanges of arboreal trunk-climbing birds such as *Melanerpes* and *Dryocopus* and its corresponding lack of development on many predatory birds, and on similarly clawed mammals, suggest that this feature in *Deinonychus* is more similar to at least some arboreal trunk-climbing birds rather than taxa that used their claws for primarily predatory behavior. This keel, along with the inner claw arc measurements as previously identified by Manning et al. (2006) and Feduccia (1993), suggest these features of *Deinonychus* may be functionally correlated with arboreal trunk-climbing behavior.

Ontogenetic variation in the curvature of the second pedal ungula - Ostrom (1976) observed that the difference in the curvatures of the two claws on *Deinonychus* specimen MCZ 4371 and *Deinonychus* specimen YPM 5205 (Fig. 3A) was not caused by distortion, but given the lack of any further comparative material, it could not

be determined whether the difference was due to individual, ontogenetic, or sexual variation.

Our comparison of claw curvature in *Velociraptor* showed that curvature in the adult IGM 100/982 is less than in the immature (Norell and Makovicky, 1997) IGM 100/985. The lack of a complete skeletal ontogenetic for any Deinonychosauridae precludes a definite conclusion, but the difference between these two *Velociraptor* specimens (Fig. 3B) suggests that curvature decreases during development.

If the more strongly curved morphology of the second pedal ungual within Deinonychosauridae indicates an immature status, and all recovered *Deinonychus* second pedal unguals in the Yale/Peabody collection possess this strongly curved character, then all specimens of *Deinonychus* within the Yale/Peabody Museum collection that are represented by recovered second pedal unguals are immature.

Limb bone histology - Periosteal rest lines revealed in thin sections from the radii of *Deinonychus* specimens MOR 1178 and MOR 1182 are similar to those found in the dinosaur *Megapnosaurus rhodesiensis* ("Syntarsus" Chinsamy-Turan, 2005). The observation of periosteal rest lines in *Megapnosaurus* was interpreted to indicate determinate growth. If, within extant endothermic taxa, and *Megapnosaurus* the presence of periosteal rest lines is an indication of determinate growth (Chinsamy-Turan, 2005) then the presence of these periosteal rest lines in the limb bones of *Deinonychus* indicates that this dinosaur may have possessed determinate growth as well.

If periosteal rest lines are most commonly found within the bones of animals that also possess endothermic metabolisms, then they can be considered an indication of endothermy. The discovery of periosteal rest lines and thus determinate growth in *Deinonychus* adds another important character to those that continue to link Dromaeosauridae to endothermy and the ancestry of avian flight (Grellet-Tinner, 2006).

The skeletal elements of *Deinonychus* MOR 1182, inferred by the presence of periosteal rest lines to represent a mature specimen, are similar in size to those of MCZ 4371 which

is the largest reasonably complete specimen of *Deinonychus*. This would suggest that MCZ 4371 represent the probable size of a fully mature member of *Deinonychus*.

Functional consequences of the re-orientation of the scapular glenoid - As Ostrom (1969) observed, the only previously known scapular glenoid of *Deinonychus* (AMNH 3015) is imperfectly preserved. Since Ostrom's original remarks, further discussions regarding the orientation and morphology of this structure were based upon either the more typical theropod scapular glenoid morphology or what was known concerning the scapular glenoid on *Velociraptor*. Reconstruction of the *Deinonychus* scapula/coracoid by Ostrom (1974) appears to have been created in accordance with what was known of other more conventional theropod osteologies such as *Albertosaurus* (Fig. 6C), *Allosaurus*, and *Gallimimus* where the glenoid has a posteroventral orientation. Subsequent interpretations (Ostrom, 1969; Ostrom, 1974; Gishlick, 2001; Senter, 2006a) were inhibited by the lack of a completely preserved scapular glenoid for *Deinonychus*.

In *Velociraptor* (pers. observ.) the glenoid is primarily ventrally facing, but it has been observed (Norell and Makovicky, 1999; Senter, 2006a) that the glenoid floor slightly extends onto the lateral surface of the scapula (Fig. 6B). This would allow the humerus to be elevated to a sub-horizontal position (Senter, 2006a), but Norell and Makovicky (1999) argue that the orientation of the scapular glenoid in *Velociraptor* would be typical for theropods and not laterally facing as in the extant avian condition. Our study of the glenoid portion of the scapula of *Deinonychus* reveals that the floor of the glenoid is rotated in closer alignment with the lateral surface of the scapula than in *Velociraptor* (Fig. 6A2).

If the articulation and orientation of the sternum and coracoid in *Deinonychus* are similar to that of *Velociraptor* (Norell and Makovicky, 1999) and *Bambiraptor* (Burnham et al., 2000), then the lateral "theropod" position of the scapula of *Deinonychus* as presented by Gishlick (2001) and Senter (2006a,b) is accurate, although the more robust morphology of the coracoid of *Deinonychus* would raise it slightly

higher dorsally than on either *Bambiraptor* or *Velociraptor*. When the coracoid and scapula of *Deinonychus* are articulated and positioned similar to *Velociraptor*, the orientation of the scapular glenoid of *Deinonychus* specimen MOR 1178 is posterolaterally facing. The dorsal edge of the glenoid would not have created an inhibiting limit or point of disarticulation for the upper rotation of the humerus.

On *Deinonychus*, the angle created by projecting the plane of the floor of the scapular glenoid to intersect with the plane of the lateral surface of the proximal end of the blade of the scapula created an angle of 35° (Fig. 6A3). This same angle in *Bambiraptor* (FARB 30556; pers. observ.) is 39° (Fig. 6A). In contrast, and as an example of what is much more typical for the orientation of the glenoid in most known theropods, the angle on *Albertosaurus libratus* (ROM 762; pers. observ.) is 65° (Fig. 6C). The alignment of these two planes on the *Deinonychus* scapula is closer than what has been discovered for similar angles found upon some extant avians such as the gyrfalcon, *Rusticolus linneaus* (BMS 6883) at 42° and the snowy owl, *Nyctea scandiaca* (BMS 7642) at 52.5°. Although the curvature of the scapula in *Bambiraptor* is somewhat greater than that in *Deinonychus* and the constricted morphology of the *Bambiraptor* coracoid is much less robust, the lateral orientations of both scapular glenoids are very similar (Fig. 6A1 & A2).

The scapulohumeral ligament and the acrocoracohumeral ligament (Baier et al., 2007) would have helped to anchor the head of the humerus within the relatively shallow open glenoid of the scapula of *Deinonychus*. These two ligaments indicate that the humerus possessed the capacity to move within an arc that would have extended both above and below the horizontal plane of the lateral extension of the forelimbs. The ligaments would also have set the limits on the vertical movement of the humerus and functioned as a complex pivot in the distribution of force from the shoulder to the forelimb. The robust scapulohumeral ligament indicates an osteologically less restricted articulation of the humerus and scapula than in the more deeply "socketed" shoulder joint of *Velociraptor*. These features appear to give the forelimb of *Deinonychus* a fairly wide arc for potential

movement including the ability to lift the forelimb some distance above the horizontal plane. Both the limitation of movement as well as the prevention of the dislocation of the humerus from the glenoid relies upon the firmness of the attachments of the acrocoracohumeral (Baier et al., 2007) and scapulohumeral ligaments (pers. observ.) rather than osteological limitation due to the lateral extension of the dorsal edge of the glenoid.

While the angle created by the intersection of the projecting of the plane of the floor of the scapular glenoid with the plane of the lateral surface of the proximal end of the blade of the scapula on *Velociraptor* is 41° and thus retains an angle similar to that found in *Bambiraptor* and to a lesser degree *Deinonychus*, what increases the ventral orientation in *Velociraptor* is a complex series of twisting curves along the main rostrocaudal axis of the scapula/coracoid complex.

The rostrocaudal axis of the scapula/coracoid complex in *Albertosaurus* creates a simple "C" shaped curve in ventral view which follows the curvature of the ribcage. In *Deinonychus*, as can be determined by the curvature of the coracoids and the curvature of the acromial process on the scapula, the curvature of the scapula/coracoid complex may be slightly more pronounced than on the larger theropods, but it is still a "C" shaped curve, as is also the case for *Bambiraptor*. The morphology of the rostrocaudal axis of the scapula/coracoid complex in *Velociraptor* deviates from this "C" shaped curvature and instead exhibits a sinusoidal curvature (Fig. 6B1) due to a lateroventral "twisting" of the proximal end of the scapula and the distal end of the coracoid, creating a ventrolateral curvature of the acromial process. This curvature is so great that for the coracoid to successfully articulate with the sternum, rostral to the coracoidal portion of the glenoid, the remaining rostral extension of the rostrocaudal axis of the coracoid must reverse direction from the lateral curvature of the acromial process of the scapula, and then create a secondary curvature as it descends in a ventromedial direction in order to articulate with the sternum.

The ventrolateral curvature of the acromial process of *Velociraptor* (Fig. 6B1 & B2)

is approximately parallel to the inner curvature of the glenoid. This results in a posteroventral orientation of the glenoid of *Velociraptor* that is not the retention of the more primitive theropod character but is a secondarily derived re-orientation of the posterolateral orientation as is found in *Deinonychus* and *Bambiraptor*.

The depth of the glenoid of *Velociraptor* is enhanced by the robust development of a rostral coracoidal tuber and a less robust caudal scapular tuber. The deep embayment of the glenoid of *Velociraptor* as well as the development of these associated tubers would probably have restricted the arcs of movement of the humerus in *Velociraptor* to a greater degree than the movement of the humerus in *Deinonychus*.

Robust deltopectoral crest on the humerus - When compared within the clade of theropods that include *Ornitholestes* as well as the Dromaeosauridae, given the relatively more basal position of *Ornitholestes* (Fig. 7A), the distal extension of the deltopectoral crest appears to be a primitive condition for the morphology of the proximal end of the humerus.

The avian supracoracoideus muscle creates a high velocity rotation of the humerus on its axis, an important component of the forelimb movement that contributes to modern avian flight (Ostrom et al., 1999). The deltopectoral crest of *Archaeopteryx* lacks of the external tuberosity on the proximal end of the humerus that is the avian humeral insertion point of the supracoracoideus muscle (Ostrom, et al. 1999). Since *Archaeopteryx* was believed to be capable of at least limited powered flight Ostrom et al. (1999) suggested that this was made possible by the presence of a particularly robust pectoralis muscle implied by the robust deltopectoral crest on the humerus of *Archaeopteryx*. The similarity in deltopectoral crests between *Deinonychus* (Fig. 7B) and *Archaeopteryx* may imply that *Deinonychus* also possessed a robust pectoralis muscle that was much larger than on *Velociraptor* (Fig. 7D) or *Bambiraptor* (Fig. 7E). The distally extended deltopectoral crest and robust pectoralis muscle in *Ornitholestes* (pers. observ.) and *Deinonychus* may represent additional features associated with the evolution of powered flight in *Archaeopteryx*. We conclude that within this clade of theropods, reduction of the

deltopectoral crest in *Velociraptor* and *Bambiraptor* represents a derived state that is also exhibited on the proximal end of the humerus of the newly described dromaeosaurid *Austroraptor cabazai* (Novas et al., 2008).

Proximal lateral flanges on first phalanx of second manual digit - Development of posterolateral flanges on the proximal phalanx of the second manual digit in *Sinornithosaurus millenii* was interpreted by Paul (2002) as evidence of anchoring of aerodynamic flight feathers and a level of powered flight greater than that of *Archaeopteryx*. However, the presence of these flanges in adult *Deinonychus* (Fig. 8A) weighing approximately 60–75 kilograms (Ostrom, 1969) suggests that they are not necessarily correlated with flight ability. Comparable flanges do not occur on IGM *Velociraptor*, 100/986 (Fig. 8B).

CONCLUSIONS AND SPECULATIONS

We conclude from our observations and comparisons with other dinosaurs and birds that:

- (a) Arboreal behavior was probable in some members of Dromaeosauridae
- (b) *Deinonychus* possessed determinate growth
- (c) The scapular glenoid of *Deinonychus* is posterolaterally oriented and possesses a robust scapulohumeral ligament fossa
- (d) The scapular glenoid orientation on *Velociraptor* is not the retention of the primitive condition as is found in some other more typical theropods but is secondarily derived.
- (e) The radius of *Deinonychus* retains informative histological data on growth and development.

Along with fusion of the coracoid and scapula in *Velociraptor*, the lack of a scapulohumeral ligament fossa, the presence of both coracoidal and scapular tuberosities and the re-orientation of the scapular glenoid in the scapula/coracoid complex together indicate that *Deinonychus* and *Velociraptor* may have possessed differences in the predominant mode of the functioning of the forelimbs. Whereas *Deinonychus* engaged in at least partial arboreal behavior, these scapula/coracoid characters on *Velociraptor* may have resulted in an increase in the body weight-bearing potential for the fore-

limbs and might have been associated with more quadrupedal terrestrial behavior.

Given Feduccia's (1993) observations regarding the relationship between the inner arc curvature of avian claws and arboreal behavior, the reduction of curvature in the second pedal ungual of *Deinonychus*, as well as being an indication of maturity, may imply a less arboreal and more terrestrial life style as an individual approached maturity. An example of a similar hatchling/arboreal and adult/terrestrial life style can be observed in the extant taxon, *Varanus komodoensis* (Komodo dragon) (Imansyah, 2007), a taxon that also possesses the inner arc curvature on its claws correlated with arboreal climbing (pers. observ.). The discovery of mature-sized teeth of *Deinonychus*, found in association with the several skeletal remains of *Tenontosaurus tilletti* (pers. observ.) as well as the discovery of possible *Deinonychus* eggshell encased in mudstone (Grellet-Tinner and Makovicky, 2006), both strongly point toward terrestrial behavior at least at the time of sexual maturity but do not contradict the possibility of juvenile arboreal behavior.

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