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Paleontological Contributions

October 30, 2015 Number 14

THE FIRST GIANT RAPTOR (THEROPODA: DROMAEOSAURIDAE) FROM THE HELL CREEK FORMATION

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ABSTRACT

Most dromaeosaurids were small- to medium-sized cursorial, scansorial, and arboreal, sometimes volant predators, but a comparatively small percentage grew to gigantic proportions. Only two such giant "raptors" have been described from North America. Here, we describe a new giant dromaeosaurid, *Dakotaraptor steini* gen. et sp. nov., from the Hell Creek Formation of South Dakota. The discovery represents the first giant dromaeosaur from the Hell Creek Formation, and the most recent in the fossil record worldwide. A row of prominent ulnar papilli or "quill knobs" on the ulna is our first clear evidence for feather quills on a large dromaeosaurid forearm and impacts evolutionary reconstructions and functional morphology of such derived, typically flight-related features. The presence of this new predator expands our record of theropod diversity in latest Cretaceous Laramidia, and radically changes paleoecological reconstructions of the Hell Creek Formation.

Keywords: Maastrichtian, maniraptoran, Laramidia, flightless, ulnar papillae, paleoecology

INTRODUCTION

Dromaeosaurids were not recognized in the known fossil record until the 1920s (Matthew & Brown, 1922) and were understudied by the scientific community until the late 1960s (Norell & Makovicky, 2004). They have recently become a focal point for research on dinosaur behavior, theropod interactions, and the origin of flight in birds (Currie, 1997; Senter & others, 2004; Xu & Norell, 2006; Turner & others, 2007; Alexander & others, 2010; Sullivan & others, 2010). Dromaeosaurid theropods have been recovered from virtually every major continent (Norell & Makovicky, 2004), and are presently among the most intensively studied theropods. Asia has historically produced the greatest volume and diversity of dromaeosaurid remains (e.g., Swisher & others, 1999; Xu, Wang, & Wu, 1999; Xu & Xiao-Chun, 2001; Liu & others, 2004; Norell & Makovicky, 2004; Xu & Norell, 2006; Turner & others, 2007; Burnham, 2008; Gong & others, 2009; Sullivan & others, 2010). The majority of Asian dromaeosaurids are small, feathered, and appear to have been scansorial or completely arboreal (Xu, Wang, & Wu, 1999; Xu & Xiao-Chun, 2001; Liu & others, 2004; Xu & Norell, 2006; Turner & others, 2007; Burnham, 2008; Gong & others, 2009; Alexander & others, 2010; Sullivan & others, 2010). Small body size is a common characteristic of dromaeosaurids (Currie, 1997; Perle, Norell, & Clark, 1999; Norell & Makovicky, 2004), although four giant dromaeosaurids are known from Asia (Perle, Norell, & Clark, 1999), South America (Makovicky, Apesteguía, & Agnolín, 2005), and North America (Ostrom, 1969; Kirkland, Burge, & Gaston, 1993).

Laramidia was home to the first named dromaeosaurid, *Dromaeosaurus albertensis* (Matthew & Brown, 1922), as well as *Saurornitholestes langstoni* (Sues, 1978), *Bambiraptor feinbergi* (Burnham & others, 2000), *Atrociraptor marshalli* (Currie & Varricchio, 2004), *Hesperonychus elizabethae* (Longrich & Currie, 2009), *Acheroraptor temertyorum* (Evans, Larson, & Currie, 2013), *Yurgovuchia doellingi*

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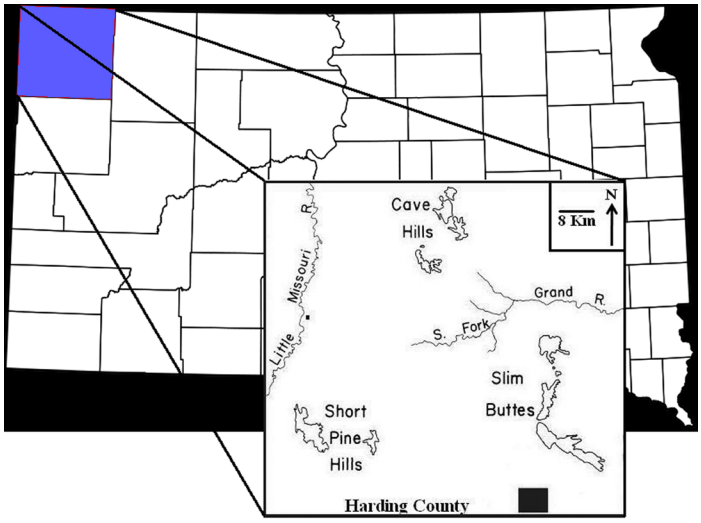


Figure 1. Map of South Dakota, and Harding County (inset). The *Dakotaraptor* study area is indicated by a black square in the southeast corner of Harding County.

(Senter & others, 2012), and the two giant dromaeosaurids *Deinonychus antirrhopus* (Ostrom, 1969) and *Utahraptor ostrommaysi* (Kirkland, Burge, & Gaston, 1993). Of these species, only three (*Saurornitholestes*, *Dromaeosaurus,* and *Acheroraptor*) are present in the late Maastrichtian (Norell & Makovicky, 2004; Evans, Larson, & Currie, 2013). Prior to this discovery, the most recent North American giant dromaeosaurid was *Deinonychus antirrhopus*, from the Aptian-Albian of the Cloverly and Antlers Formations (Ostrom, 1969; Brinkman, Cifelli, & Czaplewski, 1998; Norell & Makovicky, 2004). Gigantism occurred at least three times during dromaeosaurid evolution (Turner & others, 2007), although the selective force behind such an increase in body size thus far remains unclear.

Here, we describe the first giant dromaeosaurid from the Maastrichtian of North America, which is also the third from the North American Cretaceous, and the most recent in the fossil record worldwide. The associated remains of an adult individual were discovered by the senior author in fluvial deposits in the late Maastrichtian Hell Creek Formation of South Dakota in 2005 (Fig. 1). Other isolated bones representing a gracile morphotype of the same species, as well as isolated teeth, were discovered at another location within the same quarry. Co-occurring dromaeosaurids include *Dromaeosaurus, Saurornitholestes,* and *Acheroraptor*; however, no other theropod remains were found in the type substratum except for the holotype. The complete faunal list for this multispecific bonebed includes a diverse assortment of dinosaurs, reptiles, birds, mammals, amphibians, pterosaurs, and fish (DePalma, 2010), the majority of which are well documented in the Hell Creek Formation. Floral and stratigraphic data place the site no more than 20 meters below the Cretaceous-Paleogene Boundary, within the HCIII floral zone (Johnson, 2002).

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, USA; **BHIGR**, Black Hills Institute of Geological Research, South Dakota, USA; **IGM**, Mongolian Institute of Geology, Ulanbataar, Mongolia; **KUVP**, University of Kansas Natural History Museum and Biodiversity Institute, Kansas, USA; **NCSM,** North Carolina Museum of Natural Sciences, North Carolina, USA; **PBMNH**, The Palm Beach Museum of Natural History, Florida, USA; **YPM**, Yale Peabody Museum, Connecticut, USA.

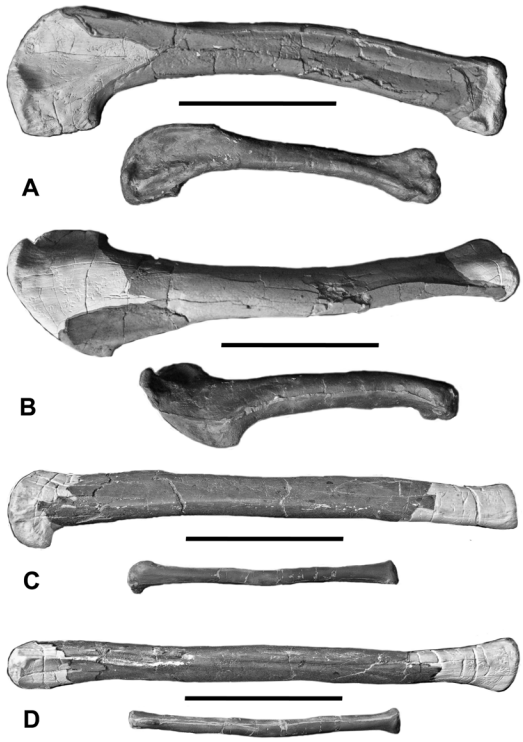


Figure 2. The humerus and radius of *Dakotaraptor* (PBMNH.P.10.113.T) compared with *Deinonychus*, top and bottom respectively. Left humeri in anterior (*A*) and lateral (*B*) views; left radii in lateral (*C*) and dorsal (*D*) views. The humerus and radius of *Dakotaraptor* are very close in morphology to *Deinonychus*, although slightly more robust. The radial sulcus of the ulna indicates that *Dakotaraptor* possessed a similar ulnar tuberosity to that of *Deinonychus*, but it is larger and more emphasized. Scale bars = 10 cm, light grey areas are reconstructed.

Anatomical Abbreviations

AL, apical length; **CBL**, crown base length; **CBW**, crown base width; **CH**, crown height; **CHR**, crown height ratio.

SYSTEMATIC PALEONTOLOGY

THEROPODA MARSH, 1881
MANIRAPTORA GAUTHIER, 1986
DROMAEOSAURIDAE MATTHEW & BROWN, 1922
DAKOTARAPTOR STEINI GEN. ET SP. NOV.

Holotype.— PBMNH.P.10.113.T, an adult individual consisting of right pedal ungual II; right pedal ungual III; right femur; left and right tibiae; left astragalus and calcaneum; left metatarsals II-IV; right metatarsal IV; one fragmentary dorsal centrum; 10 caudal vertebrae; furcula; left and right humeri; left and right radii; left

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and right ulnae; right metacarpals I and II; three fragmentary left manual phalanges.

Referred specimens.—PBMNH.P.10.115.T (gracile morphotype right tibia); PBMNH.P.10.118.T (gracile morphotype left astragalus and calcaneum); KUVP 152429 (gracile morphotype furcula), KUVP 156045 (isolated tooth) PBMNH.P.10.119.T, PBMNH.P.10.121.T, PBMNH.P.10.122.T, PBMNH.P.10.124.T (isolated teeth); NCSM 13170, isolated furcula.

Etymology.—Dakota, referring to the geographic location of the discovery as well as the Dakota First Nations Tribe, plus *raptor*, Latin for "plunderer". The specific name honors paleontologist Walter W. Stein.

Locality and horizon.—Upper Hell Creek Formation (Upper Maastrichtian), no more than 20 m below the Cretaceous-Paleogene Boundary, Harding County, South Dakota, U.S.A. The fossils were discovered in medium- to fine-grained sandstone with clay-pebble laminae that was part of a low-energy stream channel facies. While the type strata were deposited in an active fluvial system, transport energy was sufficiently low that it was not uncommon to find bones >10 cm in length from various other taxa still articulated with their adjacent elements, and plant matter that bore virtually no taphonomic alteration. In several instances, articulated or associated small vertebrate skeletons were recovered. No other theropod bones were recovered from the type substratum except for *Dakotaraptor*. Flora at the study locality places the site within the HC III floral zone (Johnson, 2002).

Diagnosis.—Dakotaraptor is diagnosed by the following characters; 1) an exceptionally large dromaeosaurid (approximately 5.5 m reconstructed adult length, estimated using the tibiae and femora of *Dromaeosaurus, Deinonychus,* and *Utahraptor* as a guide); 2) reduced flexor tubercle on pedal ungual IV; 3) lateral corial groove on pedal ungual IV is fully enclosed in a bone tube for about half of its distal length; 4) sharp ventral keel on pedal unguals II and III; 5) fibular crest is long, gracile, and its height does not exceed 9% of its total length; 6) proximal margin of fibular crest is hooked; lateral condyle of metacarpal II nearly the same size as medial condyle; 7) shallow collateral ligament fossa on lateral side of metacarpal II; 8) proximodorsal margin of metacarpal II is straight in dorsal view; 9) teeth have 15-20 denticles/5 mm on distal carina and 20-27 denticles/5 mm on mesial carina; 10) pedal ungual II (straight measurement) is approximately 29% of femur length.

METHODS

Phylogenetic analysis was performed according to the methods outlined in the Phylogenetic Analysis section. For histology, samples were taken midshaft from the robust and gracile tibias and microscopic thin sections were prepared by National Petrographic Services. The thin sections were examined with a Leica DMRX petrographic microscope at the University of Kansas. Lines of arrested growth (LAGs) were observed and counted to estimate the individual's age at the time of death; however, additional histological observations are outside the scope of this study and have been reserved for a subsequent manuscript. Utilizing a massive database compiled by Smith, Vann, and Dodson (2005), the single best resource for theropod tooth data, teeth from *Dakotaraptor* were subjected to multiple comparative analyses to exclude them from all other relevant theropod taxa from the Hell Creek Formation. Gross comparison between teeth and those of other maniraptorans was supplemented by a comparison of absolute measurements, including Apical Length (AL), Crown Base Length (CBL), Crown Base Width (CBW), Crown Height (CH), and denticle density per unit of measure. In addition, the Crown Height Ratio (CHR) and crown height vs denticle density of mid-posterior row were examined (see appendix 2), delineating the observed morphospace ranges for the theropod taxa included in the study. These multiple and integrated lines of evidence provided corroborative data on the dental taxonomy.

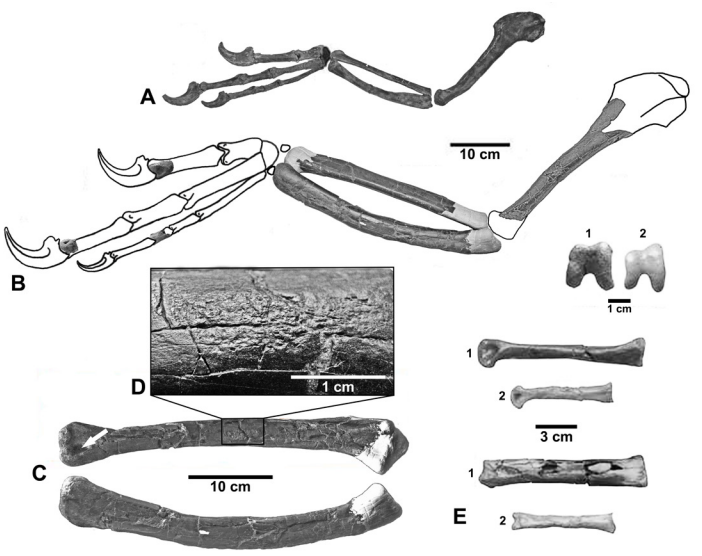


Figure 3. Wing elements of *Dakotaraptor* holotype (PBMNH.P.10.113.T) compared with *Deinonychus* (AMNH 3015, YPM 5220, YPM 5206). *A, Deinonychus* wing compared to the reconstructed left wing of *Dakotaraptor* (*B*). *C,* left ulna of *Dakotaraptor* in dorsal (top) and lateral (bottom) views, and *D,* patch of reactive bone on the ulna caused by physical trauma. Arrow points to the deep radial sulcus. E, *Dakotaraptor* right metacarpal II (*1*) compared with that of *Deinonychus* (*2*), in (top to bottom) distal, medial, and dorsal views.

DESCRIPTION

Humerus.—The left humerus (Fig. 2A, 2B; Fig. 3B) is largely intact, with minimal portions missing from the proximal and distal ends; the right humerus is present but more fragmentary, missing approximately 1/3 of the proximal end and ~1 cm of the distal epiphyses. Based on landmarks of the humerus, including the flare of the distal condyles, and width at distal margin of the deltopectoral crest, the overall dimensions of the humerus were reconstructed with some confidence. This was corroborated by examining equivalent morphology of other cursorial dromaeosaurids. The bone's conservative reconstructed length using this rationale is approximately 32 cm. The deltopectoral crest is weak where preserved, and contacts the shaft at a more gradual angle than *Deinonychus* (Ostrom, 1969) and more closely resembles *Bambiraptor* (Burnham & others, 2000) or *Dromaeosaurus*. The shaft is long, slender, and ovoid in cross-section. It curves slightly medially, similar to *Velociraptor* and *Bambiraptor,* but differs from the straighter shaft of *Deinonychus* (Ostrom, 1969).

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Table 1. Ratios of skeletal features for *Dakotaraptor*, compared to other randomly selected theropod taxa. The tibia:femur ratio is more reminiscent of *Deinonychus*, including potential cursorial agility only slightly diminished from *Dromaeosaurus*. The humerus + ulna:femur ratio is more closely allied with *Dromaeosaurus*, the taxonomically closest relative. The tibia + femur:metatarsus ratio is closest to *Bambiraptor*, indicating leverage in the distal leg and increased sprinting capability.

	Tibia:Femur	Humerus+Ulna:Femur	Tibia+Femur:Metatarsus
Archaeopteryx	1.42	2.11	3.09
Dakotaraptor	1.21	1.22	3.85
Bambiraptor	1.39	1.68	3.68
Deinonychus	1.10	1.38	4.60
Dromaeosaurus	1.37	1.29	4.10
Utahraptor	1.00	1.57	5.72

Ulna.—The left ulna (Fig. 3B, 3C) is well preserved, and measures 36 cm in length. The ulna + humerus:femur ratio is 1.22, between that of *Dromaeosaurus* and *Deinonychus*, but not quite as extreme as *Bambiraptor* (Table 1). The bone is elongate, round in cross-section, and more robust than most other dromaeosaurids, excluding *Utahraptor* (Kirkland, Burge, & Gaston, 1993) and *Achillobator* (Perle, Norell, & Clark, 1999). The proximal articular surface is damaged, but the rest of the bone morphologically resembles a more robust version of that seen in *Deinonychus* and *Dromaeosaurus*. A slight natural bow to the bone, not exacerbated by diagenesis, differs from the straighter ulna of *Bambiraptor* (Burnham & others, 2000) but resembles a similar condition in *Deinonychus* (Ostrom, 1969). The distal end is slightly broader than the shaft, flat in cross-section, and twists medially. The radial sulcus is located on the dorsal surface of the distal ulna (Fig. 3C), as in many other dromaeosaurids. It is a round concavity 2 cm in diameter and 8 mm in depth, and we may thereby deduce the maximum dimensions of the ulnar tuberosity on the radius, with which it articulates. The tuberosity for the medial collateral ligament is partially preserved just distal from the medial condyle, and is considerably more robust than that of *Deinonychus*, indicating a more fortified ligamental attachment.

The pronounced ventral ulnar ridge bears a row of 10 oblong protuberances (Fig. 4A), beginning 9.5 cm from the distal end and terminating 8.5 cm from the olecranon. They range from 8 to 10 mm in maximum length. These low, evenly spaced bosses are indistinguishable from the quill knobs, or ulnar papilli, in extant birds and other examples reported in theropod dinosaurs (Turner & others, 2007; Ortega, Escaso, & Sanz, 2010; Fig. 4), and we interpret a homologous relationship. Based on their spacing along the ulna, there is room for about 5 additional quill knobs, giving a total of 15 secondary remiges. This compares favorably with the ~12 secondaries of *Archaeopteryx* (Elzanowski, 2002; Turner & others, 2007), 14 secondaries for *Velociraptor* (Turner & others, 2007), and 18 secondaries for *Microraptor* (Xu & others, 2003; Turner & others, 2007).

The preserved portions of the proximal end indicate a triangular cross-section. The lateral and medial condyles are incomplete, but there is evidence of a shallow incisura radialis between them. A raised, localized patch of rugose bone measuring approximately 1 cm by 2.5 cm is located about midway down the shaft on the dorsolateral surface (Fig. 3D). Diagenetic and taphonomic causative agents for this roughened patch have been considered and ruled out, both lacking a favorable comparison. This area of the ulna is also not a known muscle attachment site for any known maniraptoran. The localized rugose patch is virtually identical to modern and fossil examples of reactive bone caused by physical trauma. There is no evidence that the bone had been broken in life, however it clearly experienced sufficient blunt trauma to visibly affect bone remodeling. Small portions of the right ulna are preserved, but are too fragmentary for comparison.

Radius.—The left radius (Fig. 2C, 2D; Fig. 3B) is almost entirely preserved, with a reconstructed length of 32 cm based on comparison with other dromaeosaurids and its articulation with the ulna. Only small portions of the right radius are preserved. The radius is relatively straight, and sub-circular to D-shaped in cross-section. The distal end is broad and flattened, as with other dromaeosaurids. While damaged and not fully preserved in this specimen, we can deduce from the radial sulcus of the ulna that the distal ulnar tuberosity had maximum dimensions of 2 cm in diameter and 8 mm in height. Based on the nearly complete ulna, we can deduce that approximately 6 cm of the proximal radius is missing. The thin-walled, hollow cross-section common among the Theropoda is exposed by the broken end. The robust nature of the radius is more reminiscent of *Achillobator* (Perle, Norell, & Clark, 1999) and differs in this aspect from the more gracile radii of many other dromaeosaurids. Otherwise, its overall morphology compares favorably with maniraptorans such as *Deinonychus* (Ostrom, 1969) and *Velociraptor*.

Metacarpals.—Metacarpal I from the right side is preserved, but portions of both epiphyses are damaged. The bone measures 7.5 cm in length and is morphologically identical to that of *Deinonychus* (Ostrom, 1969), however it is much stouter. Metacarpal II from the right side (Fig. 3E) is well preserved and both epiphyses are present. The bone is 13 cm in length, the shaft is more straight-sided in dorsal aspect than that of *Deinonychus*, and the distal condyles do not flare laterally. The medial distal condyle is slightly more pronounced than the lateral, however the size difference is not as pronounced as in *Deinonychus*. In distal aspect, the articular surface is almost identical to that of *Deinonychus* and *Bambiraptor* (Burnham, 2004; Fig. 3E), albeit more robust. The gingylmus displays a similarly limited range

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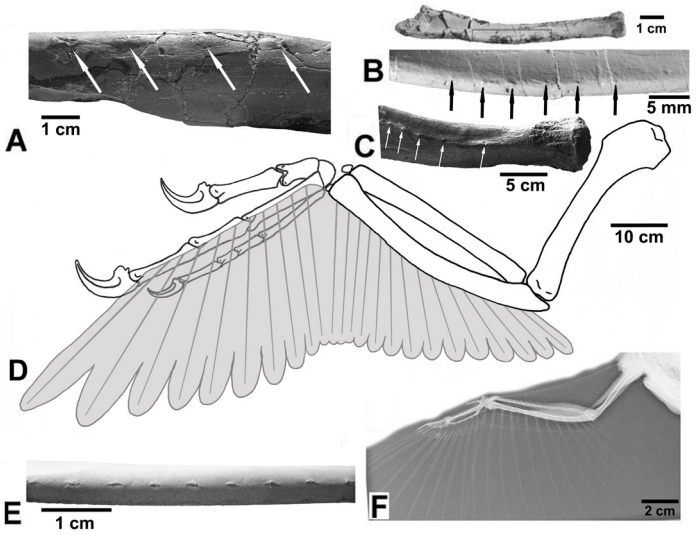


Figure 4. Reconstructed *Dakotaraptor* wing and plumage, with avian and theropod comparisons. A, enlarged view of the quill knobs on the *Dakotaraptor* holotype ulna (PBMNH.P.10.113.T), compared with quill knobs in *Velociraptor* (*B*) and *Concavenator* (*C*); *D,* conservative reconstruction of the wing plumage for *Dakotaraptor* based on quill knob placement and comparison with other dromaeosaurid and bird wings; *E,* quill knobs on a modern Masked Booby (*Sula dactylatra*) ulna, and (*F*), X-ray of a modern Barred Owl (*Strix varia*) wing showing attachment of the remiges on the quill knobs. The flattened dorsal surface of *Dakotaraptor*'s metacarpal II would have provided a stable shelf for the primary remiges that laid across it, a possible driving force for evolving the flat surface. *B* modified from Turner and others, 2007; C modified from Ortega, Escaso, and Sanz, 2010; *F* courtesy Smalley's Animal Hospital.

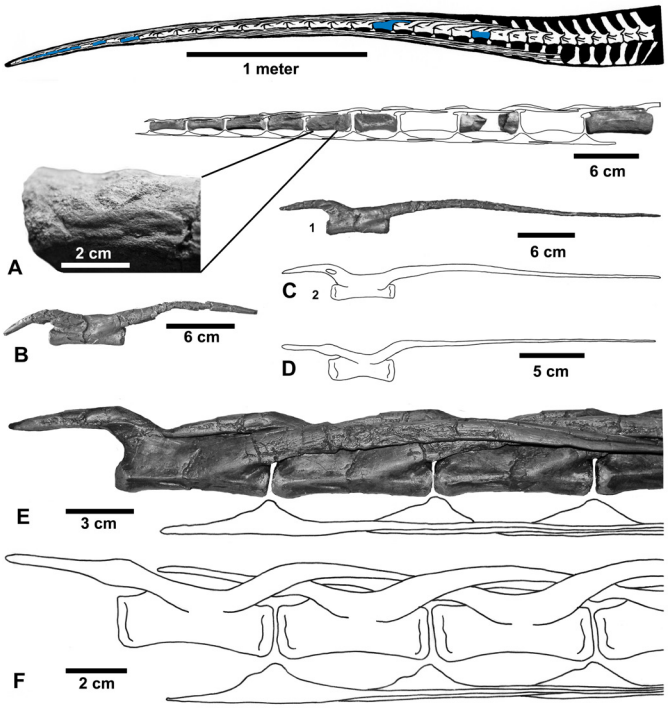


Figure 5. The tail of *Dakotaraptor* (PBMNH.P.10.113.T). *A,* (top) the ten caudal vertebrae of *Dakotaraptor* in their estimated reconstructed context (shaded blue) based on fossils of *Velociraptor* and *Deinonychus* (our most complete large dromaeosaur tails to date); (bottom) eight distal caudal centra in their approximate positions; (insert) detail of rugose pathological reactive bone on one of the centra. The most complete caudal vertebra is shown unrestored (*B*), as a restored, undistorted replica (*C1*), and in an interpretive drawing (*C2*), compared with an equivalent vertebra from *Deinonychus* (*D*). A stacked succession of articulated replicas (*E*) compares favorably with the tail of *Deinonychus* (*F*). *D* and *F* modified from Ostrom, 1969.

of motion as that observed in *Bambiraptor, Deinonychus* (Ostrom, 1969), *Velociraptor*, and other dromaeosaurids. The medial fossa for the collateral ligament is equally pronounced as that of *Deinonychus*; however, the lateral fossa is shallower. Overall, the shaft is more dorsoventrally compressed relative to other dromaeosaurids (Fig. 3E), with a much flatter shelf-like dorsal surface. The proximal end of the bone is subtriangular in cross-section, as with other dromaeosaurids. A prominent ridge extends from the dorsolateral margin of the proximal end for about 1/3 the length of the entire bone. A similar ridge is seen in *Deinonychus*, but it is more pronounced in *Dakotaraptor*. The proximodorsal margin is virtually straight in dorsal aspect, compared to the sinusoidal margin in *Deinonychus*.

Manual phalanges.—Only very fragmentary examples of the left manual phalanges were recovered (Fig. 3B), including distal articular fragments of phalanges I-1; II-2; and III-2. The bones are too fragmentary for extensive comparison, however the ligamental fossae and limited range of motion compare favorably with other members of the Dromaeosauridae, suggesting similar manual anatomy. Using the wing proportions of *Deinonychus* (Ostrom, 1969), *Dromaeosaurus*, and other large dromaeosaurids as a guide, *Dakotaraptor* possessed a wingspan of approximately 120 cm. Primary remiges would have noticeably lengthened the total wingspan but without the remiges for observation, this value must remain qualitative.

Vertebrae.—The axial skeleton is represented by 10 fragmentary caudal vertebrae (Fig. 5) and one fragmentary dorsal vertebral centrum. The dorsal centrum measures 5 cm long by 4 cm wide, with reconstructed dimensions of 7 cm long by 4.5 cm wide. The bone is highly pneumatized and thin-walled, with extensive large-celled tuberculae characteristic of the Theropoda.

The most complete vertebra is from the mid-proximal caudal series (Fig. 5B, 5C). It consists of an elongated 7 cm long centrum with a low, elongate neural arch that lacks dorsal or transverse processes, yet possesses hyper-elongated prezygapophyses characteristic of the Dromaeosauridae. None of the zygapophyses are complete, however the longest prezygapophysis is 13 cm long and resembles that of *Velociraptor* and other dromaeosaurids. The prezygapophysis has a flattened oval cross-section proximally, as with *Deinonychus* (Ostrom, 1969), and becomes rounder distally. The medial surface of the longest prezygapophysis is damaged, so it is unclear how far down the shaft bifurcation occurred or if the facet resembles that of *Deinonychus*. The broken terminus is round in cross-section, indicating that it is beyond the bifurcation (Ostrom, 1969). The diameter of the broken terminus is 4 mm, suggesting that the process extended for a considerable length further. Comparison with the dimensions of equivalent caudal vertebrae in *Velociraptor* and *Deinonychus* suggests that the prezygapophyses could have extended to overlap as many as 10 preceding segments (Ostrom, 1969), with a reconstructed

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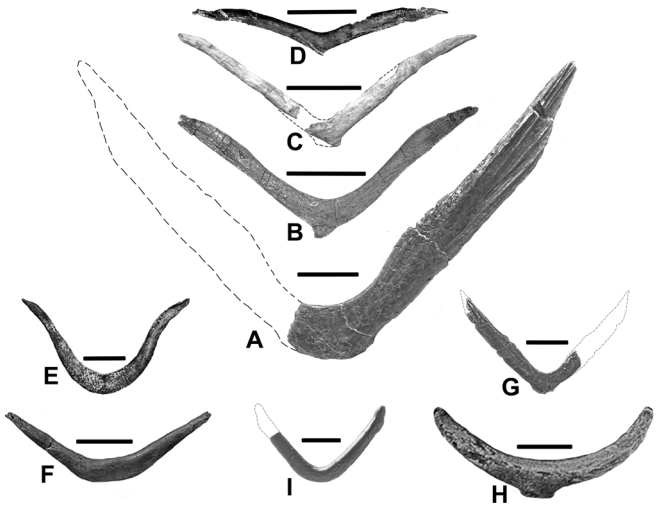


Figure 6. The furcula of *Dakotaraptor* (PBMNH.P.10.113.T) with other comparative furculae. *A, Dakotaraptor* holotype furcula compared with *Suchomimus* (*B*), *Velociraptor* (*C*), *Allosaurus* (*D*), *Gorgosaurus* (*E*), *Tyrannosaurus* (*F*), a second *Dakotaraptor* furcula (NCSM 13170) from south of the type strata (*G*), *Conchoraptor gracilis* (*H*), and an unidentified maniraptoran furcula from the Hell Creek Formation (BHI-5159; I). Dotted restorations are based on reflections of the preserved portions. Scale bars: *A* = 2 cm; *B* = 8 cm; *C* = 2 cm; *D* = 8 cm; *E* = 4 cm; *F* = 8 cm; *G* = 3 cm; *H* = 2 cm; *I* = 2 cm.

length of up to 70 cm. The postzygapophyses are preserved nearly to their termini, with a reconstructed length of 5.5 cm and a slight ventral bow. Their short length and morphology are nearly identical to *Deinonychus*, and reminiscent of other Dromaeosauridae. The articular surfaces of the centrum are amphiplatyan, suggesting the same semi-immobile condition seen in other large dromaeosaurids. The articular configuration of this vertebra is apparent when several restored replicas of it are stacked in succession, displaying an overlapping and interlocking network of zygapophyses virtually identical to *Velociraptor* and *Deinonychus* (Fig. 5E, 5F). The ventral surface of all the centra are characterized by a pronounced longitudinal furrow virtually identical to that observed in *Deinonychus* and typical for the Dromaeosauridae (Ostrom, 1969).

Another centrum from a position ~5 to 6 vertebrae proximal of the previous example is fragmentary but possesses the same general morphology. Approximately 4.5 cm of the ~7.5 cm-long centrum is preserved. The same ventral furrow is apparent, although less pronounced, and the height of the centrum, 3.5 cm, indicates a much more dorsoventrally broad proximal tail.

A series of 8 fragmentary distal caudal vertebrae (Fig. 5A) preserve nearly complete centra and partial neural arches. The vertebrae are long and narrow, and possess the same ventral furrow as the other caudal vertebrae, but the zygapophyses are not preserved. One centrum has a large roughened patch of reactive bone indicative of healed trauma (inset in Fig. 5A). The proportions of these vertebrae are consistent with the distal caudal series (~ between positions 30 and 40) of the reconstructed tail based on comparison with *Deinonychus* and *Velociraptor*.

Furcula.— The furcula of *Dakotaraptor* (Fig. 6A) was found close to the wing elements of the holotype (See quarry map in appendix 3). The furcula is morphologically distinct from tyrannosaurids and oviraptorids, the only other theropods in the Hell Creek Formation large enough and known to have possessed furculae. The left ramus, symphysis, and a miniscule portion of the right ramus are preserved. The ramus is very anteroposteriorly compressed, as with most dromaeosaurids, and has a flattened almond-shaped cross-section throughout its length. This differs from the more rounded cross-sections of the Tyrannosauridae and Oviraptorosauridae. The ramus is ~10 cm in length, straight, and does not have an expanded epicleideal process; rather, the epicleideal process tapers to a blunt point. This condition is markedly different than the laterally curved epicleideal process of the Tyrannosauridae (Fig. 6E, 6F) and the more rounded epicleideal process of the Oviraptorosauridae (Fig. 6H). The posterior surface of each ramus bears a row of small foramina, similar to the single pair seen in *Bambiraptor* (Burnham, & others, 2000) and indicating possible pneumaticity in the furcula, as with *Buitreraptor* (Makovicky, Apesteguía, & Agnolín, 2005), Aerosteon (Sereno & others, 2008; Nesbitt & others, 2009), and possibly *Bambiraptor* (Nesbitt & others, 2009). Deep parallel grooves present on the anterior and posterior surfaces of the rami, extending for approximately 1/3 of the distal length, provide more surface area for ligamental attachment and differ from the condition seen in many dromaeosaurs and other small theropods yet resemble the condition seen in many extant birds (Nesbitt & others, 2009) and some dinosaurs such as *Suchomimus* (Fig. 6B). In lateral view, the rami are straight and do not bow posteriorly as in some dromaeosaurids and other theropods such as oviraptorids. At the symphysis, a low, broad hypocleideum is present. The hypocleideum differs from the thicker, more pointed hypocleidea of the oviraptorids, and more closely resembles the incipient hypocleidea of some dromaeosaurids such as *Buitreraptor, Microraptor, Bambiraptor,* and *Sinornithosaurus* (Gong & others, 2009; Nesbitt & others, 2009). A shallow clavicular sulcus flanks the hypocleideum on the posterior surface, a feature shared by an undescribed theropod furcula from the Hell Creek Formation (BHI-5159; Fig. 6I) and some other theropods such as *Conchoraptor* and to a lesser degree *Bambiraptor*. The furcula possesses a sharp U-shape, similar to *Bambiraptor* but with slightly straighter rami that are reminiscent of *Velociraptor.* A mirror image of the furcula was overlaid over the incomplete bone to ascertain the interclavicular angle (86°). A second, smaller furcula (KUVP 152429) was recovered from the same substratum, over 9 meters from the holotype. This furcula preserves the symphysis and proximal portions of both rami. The incipient hypocleideum is less emphasized than that of the holotype and the bone overall is approximately 16% smaller, but otherwise the morphology is virtually indistinguishable. The interclavicular angle is 87°, similar to the holotype. An identical yet better preserved furcula was discovered at a stratigraphically equivalent site 16 miles south of the holotype. This furcula (NCSM 13170; Fig. 6G) preserves an interclavicular angle of 88°, which compares favorably with the gracile and robust morphotype furculae. With the exception of the hypocleideal morphology, all three furculae closely resemble those of *Sinonithosaurus, Buitreraptor,* and an unidentified dromaeosaurid from the Hell Creek Formation (BHI-5159; Fig. 6I). The interclavicular angles of the three *Dakotaraptor* furculae

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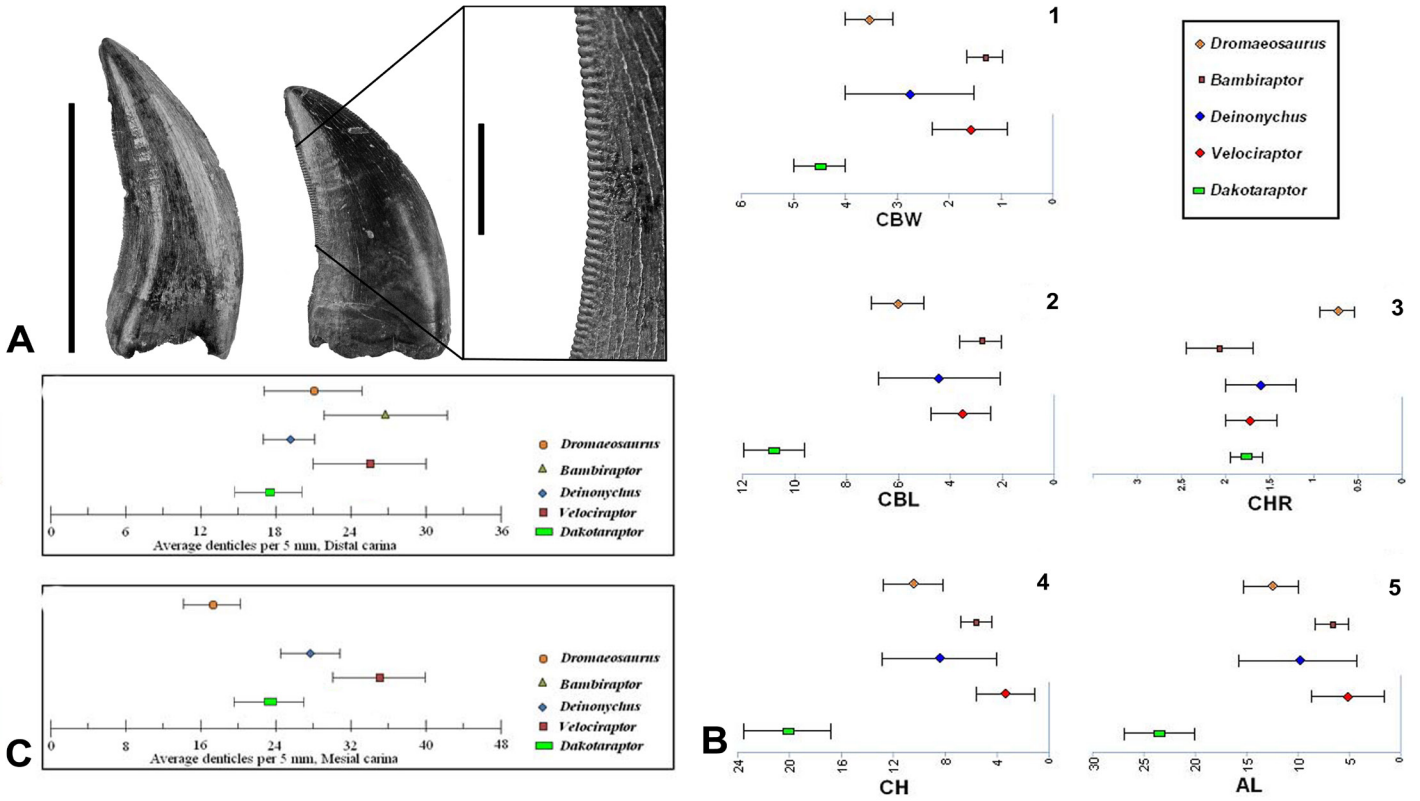


Figure 7. Dental morphometric comparison between *Dakotaraptor* and other dromaeosaurids. A, the teeth of *Dakotaraptor* (left to right, PBMNH.P.10.119.T, PBMNH.P.10.121.T, magnified denticles on distal carina for PBMNH.P.10.121.T) follow dromaeosaurid gross morphology in proportions (B 3) and density of denticles (C), but are greater in absolute size (B 1, 2, 4, 5). CBW, crown base width, CBL, crown base length; CHR, crown height ratio; CH, crown height; AL, apical length. Crown scale = 2 cm; Denticle scale = 2.5 mm; units in B are mm. Bars define the bracketed area of data, and the colored polygons are icons for specific taxa.

are very close to those of other theropods, including *Suchomimus, Velociraptor, Allosaurus, Tyrannosaurus, Gorgosaurus,* and *Conchoraptor* (Fig. 6), which possess interclavicular angles spanning 81° to 143°; however, BHI-5159 (Fig. 6I) is the closest, with an angle of 84°.

Dentition.—The teeth of *Dakotaraptor* (Fig. 7A) are strongly laterally compressed, moderately to strongly recurved, sharply tapered, and denticles are larger on the distal carina, following the general dromaeosaurid gross morphology (Norell & Makovicky, 2004). Serrations on the distal carina extend to the base of the crown, while serrations on the mesial carina typically end 1/3 of the crown's length from the base. Recently, much research has become devoted to theropod tooth morphology (e.g. Holtz, Brinkman, & Chandler, 1998; Samman & others, 2005; Smith, Vann, & Dodson, 2005). Smith, Vann, and Dodson (2005) undertook a particularly useful study, which uses tooth characters to discriminate between theropod dinosaur taxa with remarkable success. The massive data matrix of tooth characters complied by Smith, Vann, and Dodson (2005) was used to compare the teeth of *Dakotaraptor* with the maniraptorans *Velociraptor, Deinonychus, Bambiraptor, Troodon,* and *Dromaeosaurus. Tyrannosaurus,* the only other large dentulous Hell Creek theropod, was included as a control. (See Appendix 2 in supplemental information for a schematic diagram depicting the various tooth measurements.) The proportionate tooth dimensions between *Dakotaraptor* and the other dromaeosaurid taxa are universally similar (i.e. CHR; Fig. 7B.3), while the absolute size of the *Dakotaraptor* teeth universally exceeds those of all other dromaeosaurids examined (Fig. 7B.1, 7B.2, 7B.4, 7B.5). The density of denticles for *Dakotaraptor* is most comparable to those in *Dromaeosaurus* and *Deinonychus* (Fig. 7C; Fig. 8). When crown height is plotted against denticle density, a clear distinction appears between *Dakotaraptor* and other theropods (Fig. 8). While crown height for *Dakotaraptor* overlaps the lower end of the *Tyrannosaurus* spectrum, the denticle density is comparable to *Dromaeosaurus* and *Deinonychus,* not overlapping with *Tyrannosaurus* at all. *Dakotaraptor* does not overlap with any other theropod taxa examined, and the generally large size of *Dakotaraptor* teeth reliably distinguishes them from any other maniraptoran taxa in the Hell Creek Formation.

Femur.— The right femur is very intact and largely free of distortion (Fig. 9). The overall long, narrow, and gracile morphology of the femur resembles an enlarged version of *Mahakala* (Fig. 9A–C) and many other small, agile dromaeosaurids and contrasts with the stocky, robust femur of giant dromaeosaurids such as *Achillobator* or *Utahraptor* (Kirkland, Burge, & Gaston, 1993). The length is 55.8 cm, about 17% smaller than the tibia, contrary to the nearly 1:1 ratio seen in *Utahraptor* and is more similar to virtually all other dromaeosaurids (Norell & Makovicky, 2004). The shaft is anteriorly bowed (Fig. 9B, 9C), although not to the extreme of *Bambiraptor* (Burnham & others, 2000; Burnham, 2004). The femoral head is

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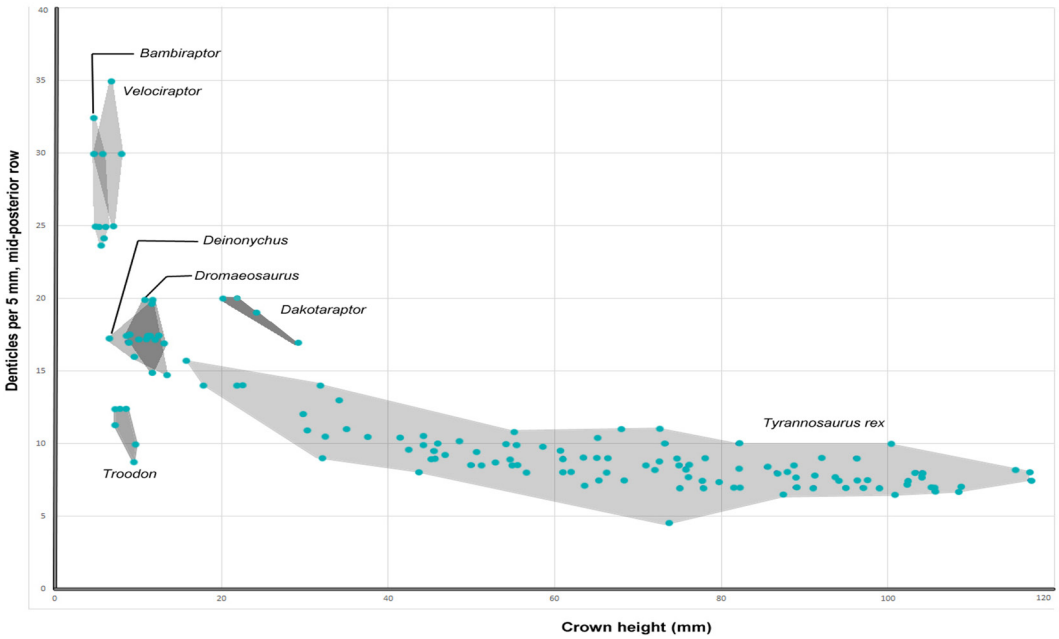


Figure 8. Comparison between crown height and denticle density for combined dentary and maxillary teeth of select maniraptorans, with *Tyrannosaurus* as a control. The maniraptorans all share somewhat low crown height (under 20 mm, excluding *Dakotaraptor*) and generally high denticle density in the mid-posterior row. *Dakotaraptor* plots within the lower crown height range for *Tyrannosaurus* but with far greater denticle density, and occupies a morphospace quite isolated and distinct from the other maniraptorans examined. Tooth data from Smith, Vann, and Dodson (2005).

subspherical and is perched at the tip of a neck (Fig. 9B). The lesser trochanter is small, as in *Saurornitholestes*, and is separated from the greater trochanter by a shallow sulcus. As in nearly all dromaeosaurids, the fourth trochanter is virtually absent, present only as a smooth, raised, elongated hump. On the posterodistal surface of the femur is a proximodistally elongated, highly rugose ridge for attachment of the adductor muscles.

Tibia, astragalus, calcaneum.— The tibia is a large yet gracile bone (Fig. 10A), bearing little resemblance to the similarly sized yet far more robust tibia of *Utahraptor* (Kirkland, Burge, & Gaston, 1993), and more closely resembles those of smaller dromaeosaurids such as *Bambiraptor*, *Saurornitholestes*, and *Velociraptor* albeit much larger. Tibia length is 67.3 cm, exceeding the length of all dromaeosaurid material described in the current literature. The tibia:femur ratio is 1.21, greater than *Utahraptor* and closer to that of *Deinonychus* (Ostrom, 1969), a characteristic of heightened cursorial locomotion (Table 1; Holtz, 1995; Carrano, 1998). The bone is relatively straight and largely parallel-sided. Although the most distal portion of the cnemial crest is not preserved, its base indicates that the crest was a robust structure. A right tibia of a smaller and more gracile individual (Fig. 10B; PBMNH.P.10.115.T) was discovered approximately 10 m away from the holotype in the type substratum. The tibia, measuring 48.5 cm, is about 17% smaller than that of the holotype and possesses the same anteriorly hooked fibular crest. The cnemial crest on the smaller tibia is nearly fully intact and about as robust as that reconstructed for the holotype. The lateral condyle on the proximal end is somewhat reduced, and is about the same diameter as the cnemial crest's basal width. One of the more striking characters of the tibia is the morphology of the fibular crest. Contrary to other theropods, the proximal margin of the fibular crest bears a proximally oriented hook (Fig. 10A.1; Fig. 10B.1, 10B.2). The hook is less pronounced in the holotype tibia, and both the hook and width of the entire fibular crest are larger in the smaller PBMNH.P.10.115.T. The hooked fibular crest has not been documented in any other dromaeosaurids or theropod dinosaurs of any kind and is among the most distinguishing autapomorphies of *Dakotaraptor*. A foramen enters the shaft of the tibia on the posterior side of the fibular crest.

The difference in size between the two preserved *Dakotaraptor* tibiae, which we shall refer to as the robust (holotype) and gracile (smaller) morphotypes, was initially attributed to representation of different stages in maturity. The well-formed epiphyses and dense, smooth bone surfaces of the smaller tibia, however, suggest that it was from an adult individual. Histological samples were taken from both tibiae, approximately midshaft. Both animals possess a comparable number of intracortical growth lines (= lines of arrested growth) indicate that they came from animals of approximately the same age (Fig. 10E). In both specimens, we see the first vestiges of the much darker and denser External Fundamental System (EFS) capping the outer cortex. This dark band represents a relatively avascular subperiosteal bone formation composed of multiple closely spaced LAGs that appears in individuals that have reached the plateau of their skeletal growth (Cormack, 1987; Padian, Werning, & Horner, 2015). Secondary osteons are virtually absent, and are limited to a narrow area along the inner cortex. Combined, these features indicate that both individuals were of near-identical age and had reached adult size, yet were young enough at death to lack extensive remodeling by secondary osteons.

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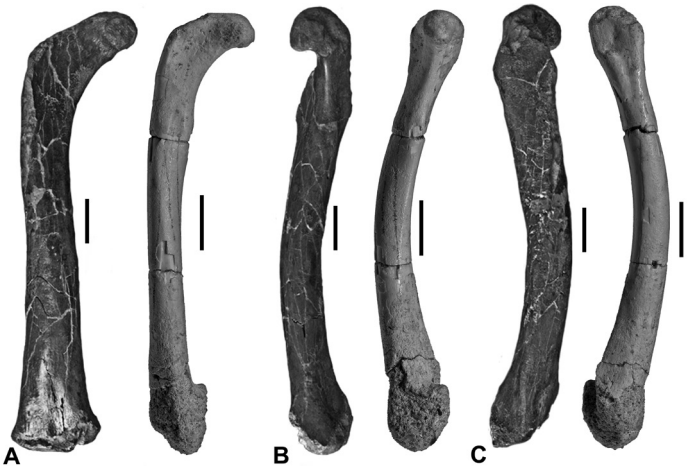


Figure 9. *Dakotaraptor* holotype (PBMNH.P.10.113.T) femur (left) compared with *Mahakala omnogovae* (IGM 100/1033; right, reversed). Femora shown in (*A*) dorsal, (*B*) medial, and (*C*) lateral views. The femur of *Dakotaraptor* retains the elongate and gracile proportions of the smaller raptor despite *Dakotaraptor*'s much larger size. The two femora also share a similar low-angle connection between the femoral head and the shaft, and a noticeable anteroposterior bow to the shaft. *Dakotaraptor* scale bars = 6 cm; *Mahakala* scale bars = 1 cm. *Mahakala* images courtesy Mike Ellington and Mark Norell, AMNH.

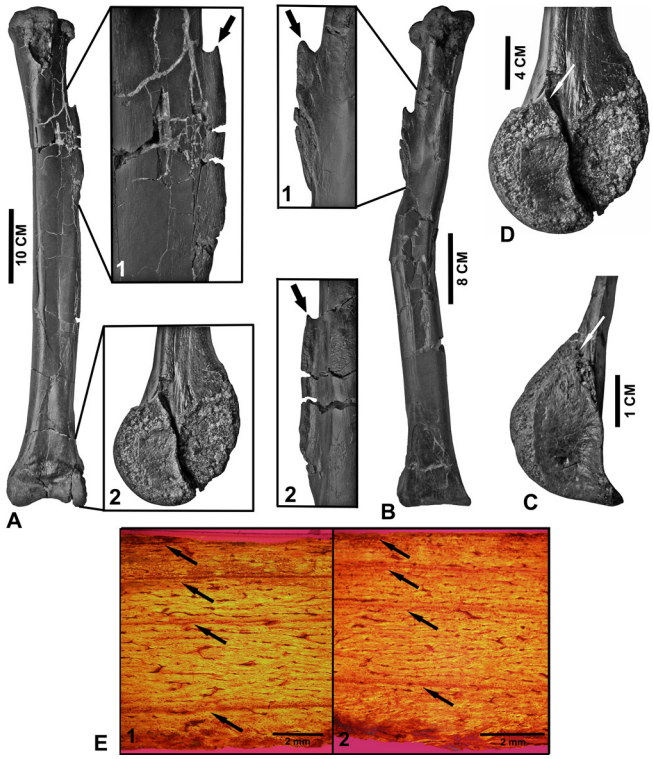


Figure 10. *Dakotaraptor* holotype (PBMNH.P.10.113.T) tibia compared to that of the gracile morphotype from the same locality (PBMNH.P.10.115.T). The holotype left tibia is shown in anterior view (*A*), with a magnified fibular crest (*1*) showing hooked proximal end (arrow in *1*) and a lateral closeup of the calcaneum in articulation with the tibia (*2*). The gracile morphotype tibia (*B*) bears the same diagnostic anteriorly hooked fibular crest (*1*) as the robust morphotype (*2*), a character that has not been reported in any other theropod dinosaur; *C* and *D* provide comparison between the gracile morphotype astragalus and calcaneum (PBMNH.P.10.118.T), and the robust morphotype (PBMNH.P.10.113.T), respectively. Notice the near identical morphology of the calcaneum and its reduced fibular facet (white arrows), indicating a markedly reduced distal fibula; *E,* microscopic thin sections of the robust morphotype *Dakotaraptor* tibia (*1*) and gracile morphotype *Dakotaraptor* tibia (*2*), show approximately the same number of LAGs. Bottom three arrows indicate widely spaced LAGs and top arrow indicates darkened band of the External Fundamental System (EFS), composed of an indeterminate number of closely packed LAGs. The presence of EFS indicates that both individuals approached the plateau of skeletal growth, while the near absence of secondary osteons (small band along inner cortex near scale bar) indicates that they were still young enough to lack extensive remodeling. The similarity in LAGs indicates that the individuals were of comparable age at the time of death. As such, the difference in tibia length is likely due to a factor such as sexual dimorphism rather than difference in age or skeletal maturity.

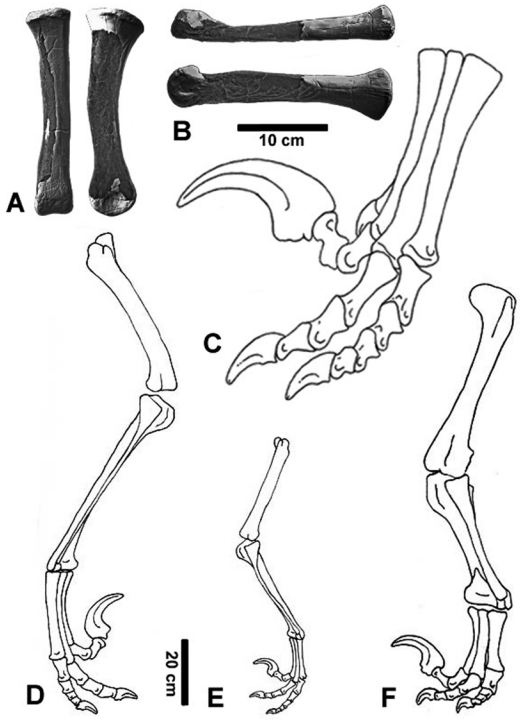


Figure 11. *Dakotaraptor* reconstructed hind limb. *A,* restored left metatarsal II in dorsal (left) and lateral (right) views, and restored right metatarsal IV (*B*) in dorsal (top) and lateral (bottom) views for the holotype (PBMNH.P.10.113.T); *C,* inferred reconstruction of the metatarsus and foot based on comparison with *Dromaeosaurus*, *Deinonychus*, and *Velociraptor*; *D,* reconstructed hind limb for *Dakotaraptor*, compared to (*E*) *Deinonychus* and (*F*) *Utahraptor*, emphasizing the *Deinonychus*-like proportions yet the overall large size comparable to *Utahraptor*.

An astragalus and calcaneum complex from the left leg (Fig. 10C) was discovered for the gracile morphotype as an isolated find approximately 9 m away from the holotype, and it is identical to, albeit smaller than, that of the holotype. The gracile morphotype astragalus and calcaneum complex measures 6 cm lateromedially, indicating a tibia length of 38.4 cm, nearly 50% smaller than the holotype, and from a slightly smaller individual than the gracile morphotype tibia. The astragalus and calcaneum are fused in the

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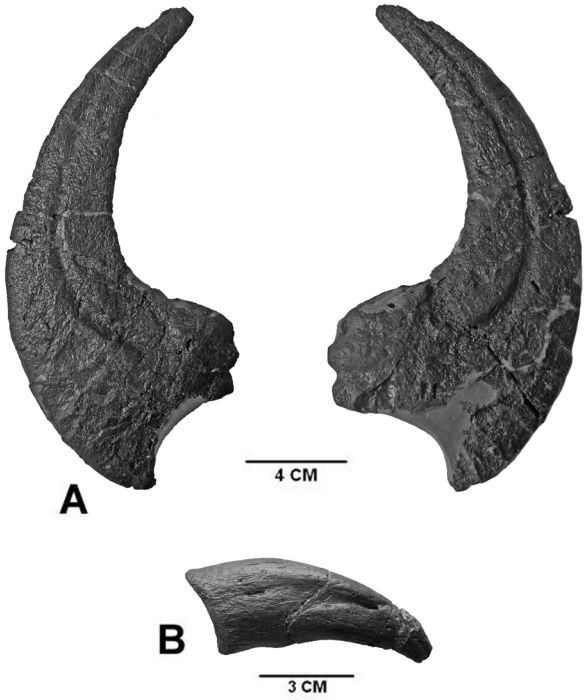


Figure 12. Pedal unguals from the *Dakotaraptor* holotype (PBMNH.P.10.113.T). *A,* the right raptorial pedal ungual II in lateral (left) and medial (right) views; *B,* right pedal ungual from digit III in lateral view. Note the bony tube that encloses the distal portion of the corial groove.

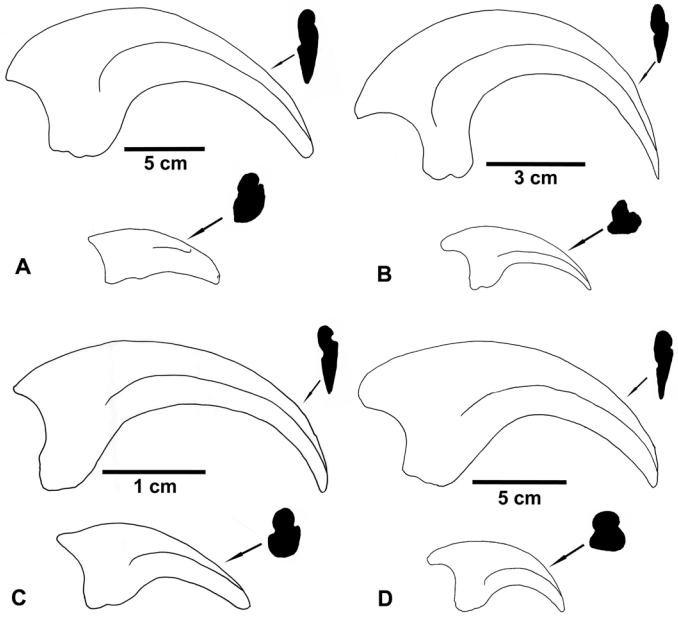


Figure 13. Comparative cross-sections of maniraptoran pedal unguals II (upper) and III (lower), taken from the same respective points along the claw. *A, Dakotaraptor*; *B, Deinonychus*; *C, Bambiraptor*; *D, Utahraptor*. Corial groove depth for *Dakotaraptor*'s pedal ungual II is comparable to other dromaeosaurs, while that of pedal ungual III is comparatively de-emphasized.

referred gracile morphotype-specimen, as is the case with the type robust morphotype. The complex in the holotype is lateromedially wide, nearly twice the minimum diameter of the tibial shaft. The astragalus and calcaneum resemble enlarged versions of those seen in the smaller dromaeosaurids. The calcaneum rests entirely on the anterior surface of the tibia, similar to other dromaeosaurids yet differing from other theropods such as the ornithomimids, and the reduced articulation facet for the fibula (Fig. 10C, 10D) indicates a gracile and markedly reduced distal fibula. Contrary to the condition of most dromaeosaurids, yet similar to the condition in *Bambiraptor* (Burnham & others, 2000), the calcaneum is fused to the astragalus. The ascending process of the astragalus is nearly complete, although its tip is missing. The attachment scar on the anterior surface of the tibia indicates that the ascending process extended for slightly less than half of the tibia's length and, contrary to *Utahraptor* but similar to other dromaeosaurids, the dorsal extremity of the ascending process is asymmetrical, terminating at the tibia's lateral margin.

Metatarsals.— Metatarsal II from the left foot and Metatarsal IV from the right foot are the best-preserved metatarsals, preserving their full respective lengths (Fig. 11). Small portions of the other metatarsals are also preserved, but are far too fragmentary for comparison. Metatarsal II is 24.7 cm in length, with a 3.5 cm minimum diameter and is sub-round in cross-section. It is a stout and robust bone, but reminiscent in overall morphology to *Deinonychus*. Metatarsal IV is 29 cm in length, with a minimum diameter of 3.4 cm. It is slightly more gracile than metatarsal II and more laterally compressed, which is further emphasized by diagenetic compression. Both bones are relatively straight. Using the ratios of metatarsals II:III and III:IV of *Deinonychus*, *Bambiraptor*, and *Dromaeosaurus* as a guide, we may estimate with some confidence that the minimum plausible length for metatarsal III was ~32 cm. This produces a conservative minimum tibia+femur: metatarsus ratio of 3.85, indicating greater leverage than *Utahraptor* (~5.72) or *Achillobator*, and more comparable to *Deinonychus* (~4.6), *Dromaeosaurus* (4.1), and the smaller dromaeosaurids (Table 1).

Pedal ungual II.—Pedal ungual II (Fig. 12A) is preserved in its entirety and exhibits the typical highly modified raptorial condition characteristic of the Dromaeosauridae (Currie & Peng, 1993; Currie, 1997; Norell & Makovicky, 2004). The ungual is 16 cm long, measured straight from the ventral articular surface to tip, and 24 cm along the dorsal curve. The ungual is approximately 29% of the femur's length, proportionately larger than that of *Deinonychus*, which is about 23% of the femur's length. The ungual is highly laterally compressed with a teardrop-shaped cross-section reminiscent of *Utahraptor* but slightly more robust (Fig. 13). Pedal ungual II for *Dakotaraptor* is robust, reminiscent of *Utahraptor* and differs from the long, strongly recurved counterpart in *Deinonychus* or *Bambiraptor* (Fig. 13). The flexor tubercle (= peduncle) is robust and prominent, as in *Utahraptor* (Kirkland, Burge, & Gaston, 1993), and protrudes ventrally past the ventral articular surface. The corial grooves are asymmetrical, diagnostic of the Dromaeosauridae, and indicate that this ungual came from the right foot (Kirkland, Burge, & Gaston, 1993; Norell & Makovicky, 2004). The lateral corial groove is situated more dorsally than the medial one, and both grooves are equally trenchant (Fig. 12A; Fig. 13A).

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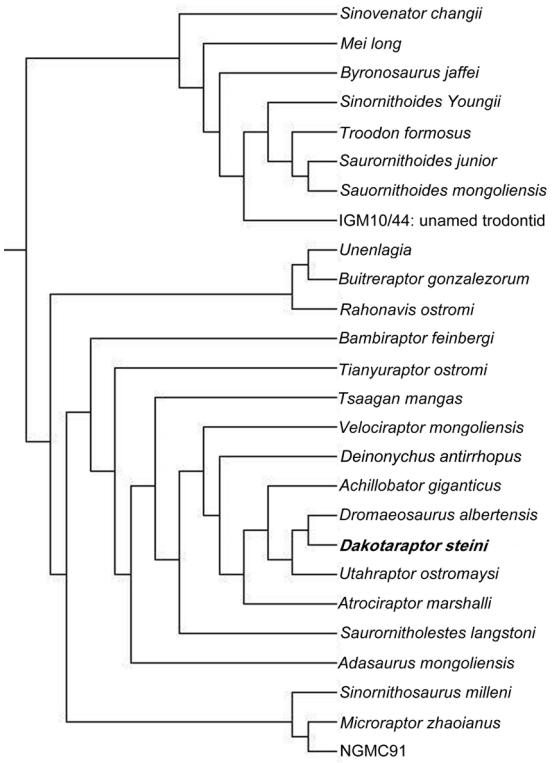


Figure 14. Phylogenetic relationships of *Dakotaraptor steini* within the Dromaeosauridae. *Dakotaraptor* is most closely allied with *Dromaeosaurus albertensis*, the most common dromaeosaurid in the Hell Creek Formation. The analysis was performed using a modified Theropod Working Group (TWiG) data set from Zheng and others, (2010).

Pedal ungual III.—Pedal ungual III (Fig. 12B) is preserved almost in its entirety, missing only a small section near the tip. The tip and main body were still adhered to the matrix in the field, so their positions relative to each other and the total length of the claw were both accurately recorded. The ungual is 7 cm long, measured straight from the ventral articular surface to the tip, and 9 cm along the dorsal curve. The proximal cross-section of the ungual is almost perfectly symmetrical, which bears more resemblance to pedal ungual III of dromaeosaurs than the typically more asymmetrical cross-section of IV, justifying its tentative assignment to ungual III. The ungual has a teardrop-shaped distal cross section with sharp ventral keel (Fig. 13), and the peduncle is reduced to near-absence. A prominent overhanging lip extends posteriorly from the proximodorsal margin as in many other dromaeosaurids. The asymmetrical corial grooves are characteristic of the Dromaeosauridae, and the more dorsal position of the right corial groove indicates the ungual is from the right foot (Kirkland, Burge, & Gaston, 1993; Norell & Makovicky, 2004; Fig. 13). The lateral corial groove is trenchant, originates as far back as the flexor tubercle, and is fully enclosed in a bony tube for approximately half of its distal length, up to the tip. This character is rare among the Theropoda and unknown in any other dromaeosaurid reported from the Hell Creek Formation. The medial corial groove is shallower than the lateral one, and is an open channel all the way to the tip.

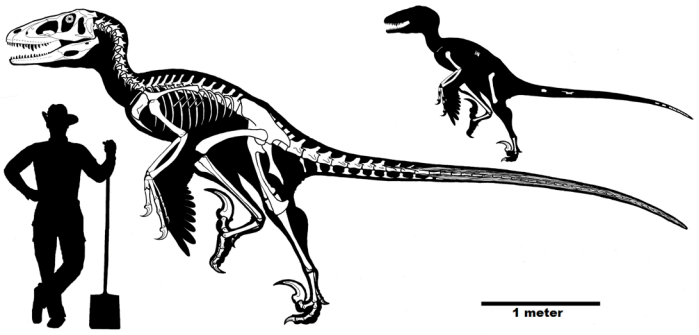


Figure 15. Skeletal reconstruction of *Dakotaraptor* holotype (PBMNH.P.10.113.T) based on available material for *Utahraptor*, *Dromaeosaurus*, *Deinonychus*, and *Achillobator*, demonstrating overall proportions and the large size of the creature. Preserved elements shown in insert.

PHYLOGENETIC ANALYSIS

Dakotaraptor was incorporated into the latest iteration of the Theropod Working Group (TWiG) data set from Zheng and others (2010). One new character was added to the data set (see Appendix 1). All characters were unordered and equally weighted. The data matrix was run in PAUP 4.0b 10 (Swofford, 2001). A heuristic search yielded 1237 equally parsimonious trees, and placed *Dakotaraptor* within the Dromaeosauridae as the sister taxon to *Dromaeosaurus* (Fig. 14).

DISCUSSION

Dakotaraptor is an exceptionally large maniraptoran (Fig. 15) and exceeds the maximum body size of all known dromaeosaurids except for *Utahraptor*, to which it is comparable. Unlike *Utahraptor* and most other giant raptor taxa, however, *Dakotaraptor* possessed body proportions more similar to the smaller, more agile dromaeosaurids. Proportions of the legs and wings are exceptionally close to those of *Deinonychus* and *Dromaeosaurus*, while the overall body size is much larger. The raptorial ungual II peduncle is emphasized, suggesting superior flexor strength comparable to or exceeding that of *Utahraptor*. Curiously, the peduncle for pedal ungual III is quite reduced, more so than all other dromaeosaurids examined here, which indicates a less rigorous usage of that ungual. The discovery of *Dakotaraptor* drastically revises our view of the Hell Creek fauna by introducing a particularly large, feathered, predatory animal into the late Cretaceous paleoecology. In the past, many researchers have formulated various reconstructions of the Hell Creek fauna based on available information (e.g. Lehman, 1987; White, Fastovsky, & Sheehan, 1998; Russell & Manabe, 2002). Recent studies have become more detailed, uncovering possible heterogeneity in the Hell Creek fauna (Bartlett, 2004; DePalma, 2010), and even including more obscure faunal members, such as insects (Labandiera, Johnson, & Lang, 2002; DePalma & others, 2010, Nel, DePalma, & Engel, 2010). All Hell Creek paleoecological reconstructions have recorded a substantial megaherbivore component composed of ceratopsians, hadrosaurs, nodosaurs, medium-sized herbivores such as pachycephalosaurs and ornithomimids, and smaller subsidiary ornithischian herbivores (Lehman, 1987; White, Fastovsky, & Sheehan, 1998; Russell &

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Manabe, 2002; Bartlett, 2004; DePalma, 2010). Hell Creek carnivorous dinosaurs have traditionally consisted of a dichotomy of large tyrannosaurids and small maniraptorans (Lehman, 1987; White, Fastovsky, & Sheehan, 1998; Russell & Manabe, 2002; Bartlett, 2004; DePalma, 2010) with a paucity of transitional size categories. The discovery of a new major predator such as *Dakotaraptor* in the Hell Creek Formation changes our view of the Hell Creek paleoecology and necessitates that our reconstructions be amended to compensate for it. The presence of two morphotypes also adds to our knowledge of dromaeosaurid body size dynamics.

The robust and gracile morphotypes represent individuals of approximately the same age and skeletal maturity. Highly emphasized intraspecific variation, developmental plasticity, and other causes are certainly viable explanations for variation in size within two individuals of comparable developmental age, however these causative agents are typically aberrations or otherwise the exception rather than the normal standard. As such, they are not universally common or widespread within a population. Sexual dimorphism, however, is universally distributed throughout a population when it is present. It would be implausibly rare to infer that of the only two examples of a rare taxon, one exhibits a rare malady or developmental variation. It is much more parsimonious to infer that the size disparity is due to a much more common (and therefore more likely to be recorded in the fossil record) factor such as sexual dimorphism (Larson, 2008) than one of the other causative agents that are exceptions/aberrations and therefore much less likely to be recorded in the fossil record. It is unresolved, however, which morphotype represents male or female.

The unusually large size of both the gracile and robust morphotypes of *Dakotaraptor,* and the possibility that it hunted in packs or family groups, as has been suggested for the Dromaeosauridae (Kirkland, Burge, & Gaston, 1993; Maxwell & Ostrom, 1995), would have had a pronounced impact on the paleoecology. *Dakotaraptor* also fills the size gap that existed between the small deinonychosaurids and large tyrannosaurid groups, forming a predatory hierarchy more reminiscent of those actually observed in nature today (Eloff, 1964; Eloff, 1984; Kingdon, 1997). *Dakotaraptor* likely fed on animals larger than the prey of the other small maniraptorans of the Hell Creek Formation, but probably not as large as the adult megaherbivores, which would have been better suited for larger predators such as the tyrannosaurids. It is conceivable, however, that *Dakotaraptor* would have been occasionally in direct competition with smaller tyrannosaurids such as immature *Tyrannosaurus rex* or *Nanotyrannus lancensis,* which, at an adult length of 6–9 m, were not much larger than *Dakotaraptor.*

The ulna of *Dakotaraptor* provides an intriguing clue to the raptor's ecology and evolutionary history. The presence of some sort of feathery integument on *Dakotaraptor*'s body was already expected based on the prevalence of feathers among the Dromaeosauridae and phylogenetic bracketing, but quill knobs on the ulna of such a large dromaeosaurid are unprecedented and indicate 1) the presence of remiges with stout rachi on the wings, and 2) sufficient use of those features to necessitate evolutionary retention of the reinforced attachment sites and not secondarily lose them. Quill knobs, a derived character related to flight that were once thought exclusive to birds, have recently been reported in a variety of theropods including oviraptorids (Lamanna & others, 2014), carcharodontosaurids (Ortega, Escaso, & Sanz, 2010), and dromaeosaurids such as *Velociraptor* (Turner & others, 2007). In modern birds, quill knobs act as ligamental attachment sites for Sharpey's fibers that provide extra support for the calamus of secondary flight feathers (Edington & Miller, 1942; Capainolo & Butler, 2010; Hieronymus, 2015). While birds possess feathers all over their bodies anchored in tracts of pterylae, quill knobs are only present on the wings, where they are critical to providing necessary additional support to remiges where they experience heightened stress during use (Edington and Miller, 1942; Capainolo & Butler, 2010). Asymmetrical flight feathers were common among small arboreal or gliding dromaeosaurids during the Early Cretaceous, and quill knobs have been identified in some primitive avian taxa (e.g. *Rahonavis*) as well as flightless descendants of such taxa (e.g. *Velociraptor*). The absence of quill knobs does not preclude the presence of noticeable remiges, as we know from numerous extant bird taxa, however the presence of quill knobs does unequivocally indicate the presence of remiges (Turner & others, 2007). The size and proportions of *Dakotaraptor* almost certainly preclude its potential for flight, negating the necessity for developing long remiges or associated quill knobs to support the rigors of flight. Rather, it is more plausible that *Dakotaraptor* descended from an evolutionary line that already possessed flight or that was already sufficiently close to attaining it that it had evolved a suite of advanced adaptations for its facilitation. *Dakotaraptor* thus represents either a secondarily flightless form, or a descendent of a maniraptoran lineage that was much more adapted for flight than *Dakotaraptor*, as has also been suggested for the quill knobs in *Velociraptor* (Turner & others, 2007). The plausibility of this scenario is more apparent when we consider the evolutionary trends in Cenozoic secondarily flightless birds. We see repeated, independent incidences in which derived characters linked to flight (i.e., remiges, quill knobs, etc.) are retained in secondarily flightless birds that had no immediate use for them (e.g., flightless Gruiformes, Psittaciformes, Columbiformes). Furthermore, a second trend we observe in secondarily flightless birds is a predisposition toward gigantism in response to the resultant shift in ecology (i.e., the ratites, phorusrhachids, Aepyornithoformes, etc.). We see both the retention of derived flight-related morphology and the shift toward gigantism trends in *Dakotaraptor*, highly suggestive that it represents a secondarily flightless form.

The ecological function of *Dakotaraptor*'s remiges may remain unknown. Contrary to the reduced limbs common in giant secondarily flightless birds, *Dakotaraptor* retained quite long forelimbs with robust bone structure. Some other researchers (e.g. Hopp & Orsen, 2004) have previously suggested that shielding eggs during brooding was a selective evolutionary force for the development of long remiges in taxa such as the oviraptorids. While longer remiges would certainly have provided potential shielding for eggs and young, this function alone would not have caused sufficient stress to necessitate the development or retainment of reinforced attachment sites (= quill knobs). Thus, this function does not fully relate to *Dakotaraptor* or its immediate ancestors even if it may have been an effective and often-employed peripheral use. There is no known practical function for *Dakotaraptor*'s remiges that would have necessitated developing quill knobs, suggesting that they are retained from one of the ancestral

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taxa. Then, what function did *Dakotaraptor* co-opt them for? Aside from brooding, examination of certain extant flightless birds suggests that they could have played a role in hunting strategy, mating display, aggressive territorial behavior, and/or shielding the young (*sensu* Cooper & Harrison, 1994; Hopp & Orsen, 2004; Longrich & Olson, 2011). Implementing feathers in aggressive territorial behavior, as has been observed for extant avian taxa (Cooper & Harrison, 1994; Longrich & Olson, 2011), is a behavior that could easily have augmented the pack-hunting strategies already proposed for *Deinonychus*, *Utahraptor*, and other dromaeosaurs (Kirkland, Burge, & Gaston, 1993; Maxwell & Ostrom, 1995). *Dakotaraptor*'s remiges would have lengthened the outstretched arms, providing long and robust outstretched wings that would have been useful when implemented in such strategies. Furthermore, the process of mantling, i.e pinning down the body of a prey animal with ungual II and stabilizing themselves using vigorous flapping motions of the wings, has been well documented in raptorial birds (Fowler, Freedman, & Scannella, 2009; Fowler & others, 2011) and was suggested as plausible behavior for *Deinonychus* (Fowler & others, 2011). It is equally plausible that *Dakotaraptor* could have engaged in similar prey acquisition behavior.

The precise evolutionary selection toward gigantism in dromaeosaurids is not well understood; however, dromaeosaurids experienced rapid size increase at least three times in the Cretaceous (Turner & others, 2007). The trend toward gigantism is exemplified by *Deinonychus*, *Unenlagia*, and *Achillobator* + *Utahraptor* (Turner & others, 2007); however, it is unclear what the selective pressure may have been. The Mesozoic was a time in Earth's history in which megaherbivores were prevalent (Bakker, 1986), and carnivorous dinosaurs likely adapted accordingly. The earliest giant dromaeosaurid is *Utahraptor*, which occurs in the Early Cretaceous of North America (Kirkland, Burge, & Gaston, 1993). As was pointed out by Kirkland, Burge, and Gaston (1993), the beginning of the Cretaceous was a transitional period for terrestrial faunas, in which there was a shift from the sauropod-stegosaur-dominated megaherbivores of the late Jurassic, to the nodosaur-iguanadontid-dominated megaherbivores of the Early Cretaceous. Whereas allosaurids and similar large predators preyed upon the late Jurassic megaherbivore fauna, *Utahraptor* helped to fill the megacarnivore niche in the early Cretaceous. It is plausible that *Dakotaraptor* filled an analagous role in the late Cretaceous ceratopsian-hadrosaur-dominated herbivore fauna of the Hell Creek Formation.

While *Dakotaraptor* is closer in size to *Utahraptor* than any other dromaeosaurid, it is probable that they filled slightly different ecological roles. Contrary to *Dakotaraptor* and most other dromaeosaurids, *Utahraptor* has a nearly 1:1 femur to tibia ratio (Kirkland, Burge, & Gaston, 1993), a proportionately shorter metatarsus, and a robust skeleton overall. Consequently *Utahraptor* likely had diminished effectiveness as a pursuit predator, or at least was limited to prey much slower than it. *Dakotaraptor* has a femur 17% shorter than the tibia and a proportionately longer metatarsus, comparable to many smaller dromaeosaurids (Norell & Makovicky, 2004). This lengthening of the distal hindlimb is associated with heightened cursorality (Holtz, 1995; Carrano, 1998) and *Dakotaraptor* likely had potential for exceptional pursuit capabilities comparable to the smaller dromaeosaurids. *Dakotaraptor* had a fortuitous combination of characters that made it a formidable predator: large body size and incredibly robust raptorial pedal ungual II similar to *Utahraptor*, and potential for speed and agility comparable to the smaller dromaeosaurids.

CONCLUSION

A giant, feathered dromaeosaurid exhibited by gracile and robust morphotypes was unexpected and thus is an important addition to the Hell Creek fauna. It fills the gap in body size distribution between the small maniraptorans and large tyrannosaurids previously documented in the formation, while adding to the known diversity of Hell Creek maniraptorans. *Dakotaraptor* also records a fourth event in which dromaeosaurids achieved atypically large body size. Moreover, the presence of quill knobs, indicative of elongate, stiffened feathers on the forearms, is unprecedented in giant dromaeosaurids and requires a reexamination of trends in quill knob evolution. The functional morphology of the long feathers, possibly of modern avian aspect as implied by known Asian forms, must also be considered. Subsequent studies of *Dakotaraptor* and the Hell Creek fauna may aid in our understanding of the circumstances that prompted dromaeosaurids to retain ligamental architecture for feather attachment, and may also provide information critical to a more accurate understanding of the lost capacity for flight.

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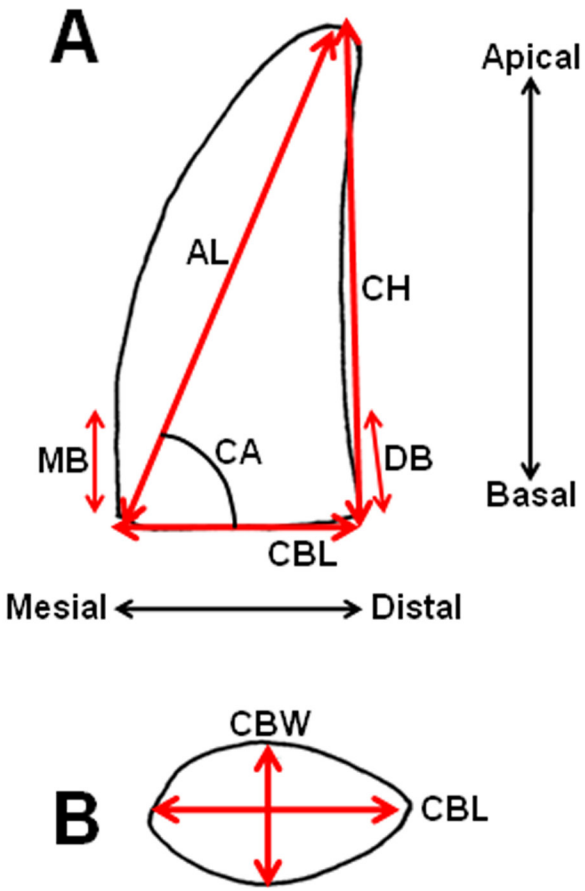
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APPENDIX 1

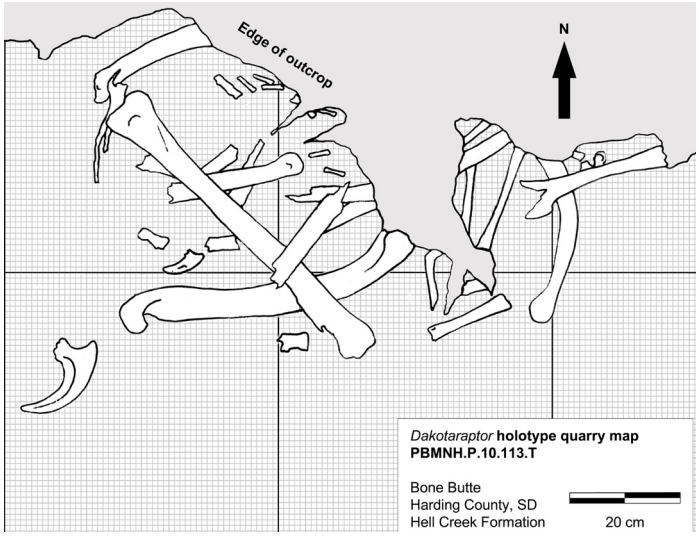
New character added to the Zheng and others (2010) data set:
Character 361: Fibular crest of tibia with smooth margins (0) or hooked proximally (1).

APPENDIX 2



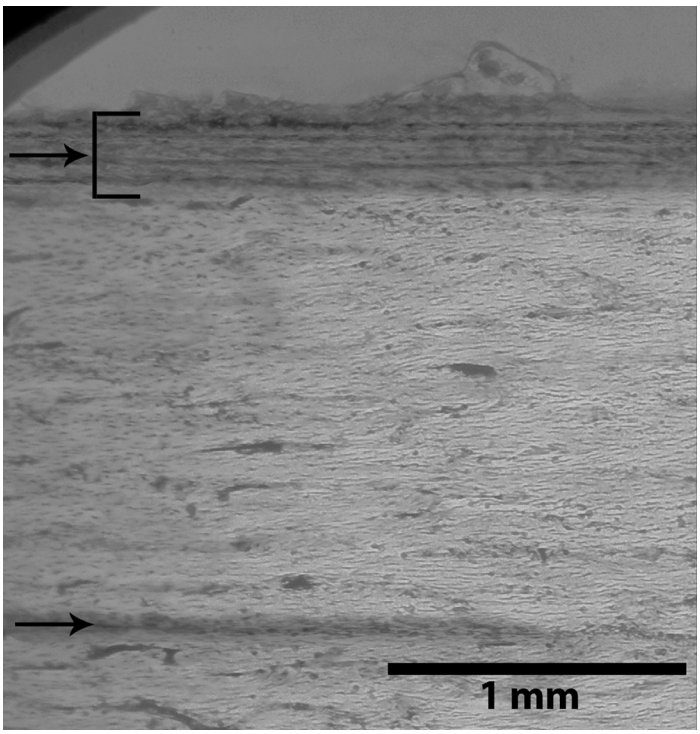
Schematic diagram depicting tooth measurements used in the present study (A, B). Abbreviations are defined in the main body of the manuscript. Diagrams modified from Smith and others (2005).

APPENDIX 3



Quary map indicating the spatial relationship of the Dakotaraptor holotype (PBMNH.P.10.113.T) bones as they were found in the field

APPENDIX 4



Magnified view of tibial outer cortex (PBMNH.P.10.113.T) showing the multiple closely packed LAGs that comprise the EFS (upper arrow) and one isolated LAG (lower arrow). This exemplifies the condition seen in all of the histology slides.

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