

A Preliminary Report on the Theropod Dinosaur Fauna of the Late Campanian Kaiparowits Formation, Grand Staircase-Escalante National Monument, Utah

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ABSTRACT

The Kaiparowits Basin Project—a joint collaboration between the Utah Museum of Natural History and the University of Utah—has made significant additions to the previously recognized theropod dinosaur fauna of the late Campanian Kaiparowits Formation of southern Utah. Results of this project include: the discovery of *Hagryphus giganteus*, the first diagnostic North American oviraptorosaur south of Montana; a nearly complete juvenile skeleton of a new genus of tyrannosaur; the first cranial remains of a Kaiparowits troodontid from the formation; and the first diagnostic ornithomimid forelimb material from the formation. Comparison of the Kaiparowits theropod fauna with other contemporaneous formations across the Western Interior Basin reveals consistency of mid-level clade diversity among theropods, yet also demonstrates species-level endemism for those groups for which diagnostic materials have been recovered.

Keywords: Late Cretaceous, Coelurosauria, Maniraptora, biogeography, Western Interior Basin

Introduction

Seven years ago, field crews of the Utah Museum of Natural History (UMNH) and the University of Utah embarked on an exhaustive research project to survey and document the Late Cretaceous dinosaur fauna of Grand Staircase-Escalante National Monument (GSENM), southern Utah, with a focus on the poorly sampled late Campanian Kaiparowits Formation (Figure 1). To date, this collaborative effort—known as the Kaiparowits Basin Project (KBP)—has met with notable success, building substantially upon the previously recognized vertebrate fauna of the formation and highlighting its significance to our understanding of dinosaur evolution within the Western Interior Basin (WIB).

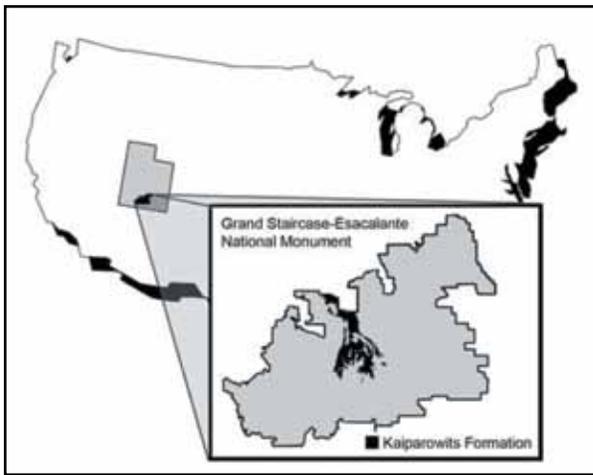


Figure 1. Map showing the location of Grand Staircase-Escalante National Monument in southern Utah, with Kaiparowits Formation outcrop illustrated in black.

Prior to the initiation of the KBP, decades of foundational microvertebrate studies were conducted in the Kaiparowits Basin. This work was predominantly achieved by Jeffrey Eaton and Richard Cifelli, who along with their colleagues established the first comprehensive faunal list for the Kaiparowits Formation (Eaton and Cifelli 1988). Recognizing the faunal list to be an underrepresentation of all but mammalian taxa (the focus of Eaton and Cifelli's research project in the area), Howard Hutchison, Jeffrey Eaton, and Michael Parrish subsequently attempted a more thorough documentation of the lower vertebrate fauna of the Kaiparowits (Hutchison 1993; Hutchison et al. 1997; Parrish and Eaton 1991), and ultimately compiled a more comprehensive faunal list including eleven dinosaur taxa (Eaton et al. 1999). These advances notwithstanding, the recognition of dinosaurian taxa within the Kaiparowits Formation has been limited almost entirely to microvertebrate and fragmentary skeletal remains. The recent work undertaken by the UMNH and the University of Utah represents the first concerted effort to collect and research the monument's dinosaurian fauna and has already added considerably to our understanding of dinosaur diversity across the WIB during the late Campanian (Gates and Sampson 2006; Smith et al. 2004; Zanno and Sampson 2005). Through description of new taxa, taxonomic refinement of previously identified theropod materials, and collection of novel skeletal elements of enigmatic taxa, this collaborative project has resulted in a more thorough reconstruction

of this unique and historically underrepresented Late Cretaceous ecosystem.

Here we review the known theropod fauna of the late Campanian Kaiparowits Formation based on materials recovered during the 2001-2006 field seasons by UMNH and University of Utah crews. For a more comprehensive review of paleontological work conducted prior to the initiation of this project, the reader is referred to Eaton and Cifelli (1988), Eaton et al. (1999), Hutchison et al. (1997), and Parrish and Eaton (1991).

Institution Abbreviations—BYU, Brigham Young University, Provo, Utah; MNA, Museum of Northern Arizona, Flagstaff, Arizona; RAM, Raymond M. Alf Museum, Claremont, California; UMNH, Utah Museum of Natural History, Salt Lake City, Utah; YPM, Yale Peabody Museum, New Haven, Connecticut.

Theropod Diversity in the Kaiparowits Formation

Tyrannosaurs

Tyrannosaurs are a group of large-bodied, highly specialized theropods that typically functioned as the top predators within Late Cretaceous ecosystems. The Maastrichtian-aged *Tyrannosaurus rex* reached body masses exceeding those of all other terrestrial carnivores (5000-6000 kg); however, tyrannosaurs from the preceding Campanian Age, although still among the largest of theropods, were typically much smaller bodied (1,000-2,500 kg).

Although late Campanian tyrannosaur diversity has been well-represented in northern WIB formations for more than a century (Lambe 1914; Osborn 1905), tyrannosaur species inhabiting southern WIB ecosystems during this interval have remained poorly understood. In fact, prior to the initiation of the KBP, the only diagnostic tyrannosaur material recovered from the Kaiparowits Formation consisted of a partial, associated skull collected by Brigham Young University in the 1970's. This specimen (BYU 9396) is currently

under study by Thomas Carr, Carthage College, and is thought to represent a new genus closely related to *Daspletosaurus*, the only tyrannosaurid recognized in the late Campanian of New Mexico (Carr and Williamson 2000).

Recent field work in the Kaiparowits Formation by the UMNH has greatly expanded our knowledge of Kaiparowits tyrannosaurs, resulting in the discovery of numerous isolated elements as well as seven associated specimens. Of the latter, an exceptionally well preserved juvenile skeleton (UMNH VP 16690), discovered in 2004, represents one of the most complete and phylogenetically informative tyrannosaur individuals thus far collected from the southern WIB formations. UMNH VP 16690 is an associated juvenile skeleton that is approximately 65% complete, preserving a large portion of the skull, numerous cervical, dorsal, sacral, and caudal vertebrae, well-preserved chevrons, cervical and thoracic ribs, nearly complete illia, pubes and ischia, a complete right femur, tibia, and fibula, and a single pedal phalanx and ungual. Most of the caudal portion of the skull has been recovered, including a complete braincase, both frontals, parietals, quadratojugals, postorbitals, and lacrimals, a single maxilla, articular, angular, surangular, dentary, and multiple teeth. A number of associated but shattered elements from the rostral portion of the skull, in addition to several shattered teeth, suggest that the facial skeleton may have been trampled prior to burial. The reconstructed body size of this individual (approximately 9 m), together with the lack of neurocentral fusion in preserved dorsal and sacral vertebrae, are suggestive of a juvenile to subadult age for the animal at the time of death (Brochu 1996). Preliminary examination of these remains indicates that UMNH VP 16690 may represent a subadult individual of the same new genus as the unnamed mature BYU specimen; however, as both of these specimens are currently under study, and the BYU specimen lacks concrete stratigraphic and locality data, more research is needed to determine their individual taxonomic and phylogenetic affiliations.

While the relationship between the BYU and UMNH tyrannosaur material has not yet been established, the general morphology of UMNH VP

16690 suggests that this tyrannosaur shares a more recent common ancestry with *Daspletosaurus* than with the other late Campanian genera *Albertosaurus* and *Gorgosaurus*. This conclusion is supported by the postorbital anatomy of UMNH VP 16690, which displays a highly developed cornual boss (even at a pre-mature ontogenetic stage) and a rostrocaudally robust jugal ramus more similar to that of *Daspletosaurus* and the unnamed New Mexico genus than to the more gracile postorbital morphology of *Albertosaurus* and *Gorgosaurus* (Figure 2). Several other features present on the skeleton of UMNH VP 16690 are also indicative of a close relationship between these genera.

Additional associated but less complete tyrannosaur individuals and isolated elements recovered during the KBP include: associated juvenile cranial material, including fused parietals, a partial unfused frontal and a partial dentary (UMNH VP 12586); partial limb elements and teeth (UMNH VP 16161); fragmentary limb elements, a pedal phalanx, and ungual UMNH VP 16692; associated limb and skull fragments, including a partial dentary, pedal phalanx, and ungual (UMNH VP 16693); a tooth, caudal vertebrae, left femur, tibia, fibula, metatarsal III, a pedal phalanx, and ungual of a large adult individual (UMNH VP 16694); isolated fused parietals (UMNH VP 16225); an isolated humerus (UMNHVP 12223); and an isolated jugal from a large adult (UMNH VP 16691).

The abundance of tyrannosaur material collected during the relatively brief time span of the KBP challenges previous statements that the late Campanian formations of New Mexico exceed those of Utah with regard to tyrannosaur preservation (Carr and Williamson 2000), and highlights the importance of the KBP in understanding dinosaur evolution in the WIB. Study of the diagnostic tyrannosaur material recovered from the Kaiparowits Formation will permit a more comprehensive understanding of tyrannosaur diversity, biogeography, and evolution during the late Campanian. In addition, the juvenile specimen UMNH VP16690 will undoubtedly lend important information to the study of tyrannosaur ontogeny and life history.

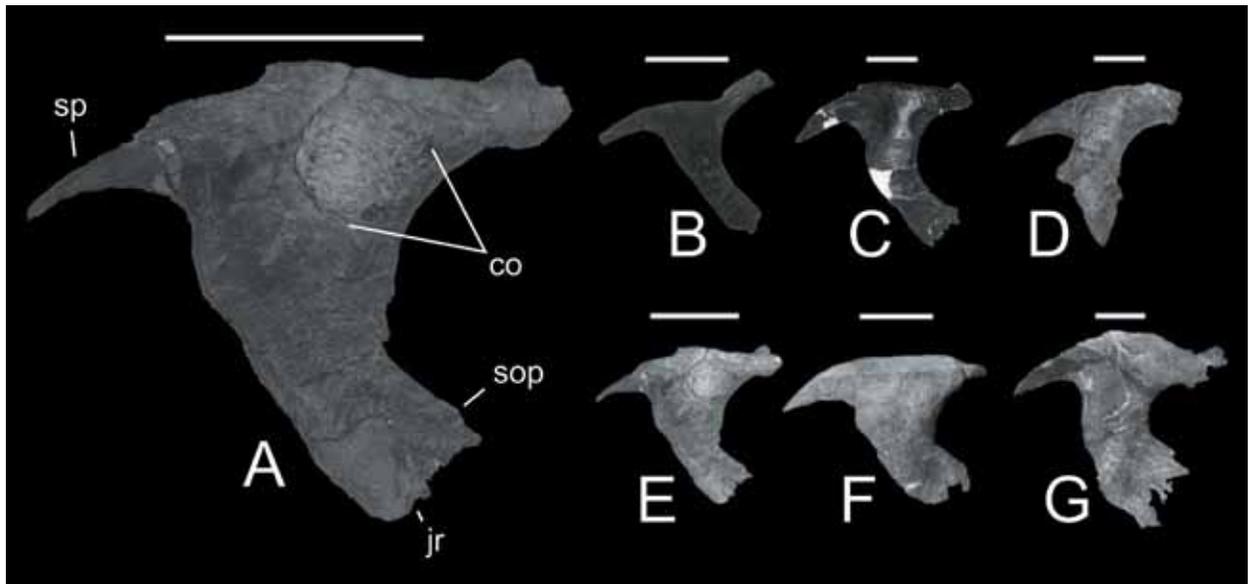


Figure 2. Morphological variation in the postorbitals of Campanian tyrannosaurs from the Western Interior of North America, all shown in right lateral view. **A** and **E**, unnamed Kaiparowits Formation tyrannosaur, UMNH VP 16690; **B**, *Gorgosaurus*, TMP 91.36.500 (reflected and modified after Currie 2003a); **C**, *Albertosaurus*, TMP 81.10.1 (reflected and modified after Currie 2003b); **D**, *Daspletosaurus*, combination of NMC 8506 and TMP 2001.36.1 (reflected and modified after Currie 2003b); **F**, New Mexico tyrannosaur NMMNH P-25049; and **G**, *Tyrannosaurus* FMNH PR 2081 (reflected and modified after Brochu 2003, image courtesy of Chris Brochu). **Abbreviations:** **co**, cornual boss; **jr**, jugal ramus; **sop**, suborbital process; **sp**, squamosal process. **B-G** scaled to approximately the same size. Scale bars equal 5 cm.

Ornithomimids

Ornithomimids (ostrich mimics) were relatively medium-bodied, lightly built dinosaurs, possessing toothless beaks, elongate necks, and hindlimbs built for cursoriality (Carrano 1999; Coombs 1978; Snively et al. 2004). They are generally regarded as near relatives of tyrannosaurs, falling within coelurosaurs but outside of Maniraptora, the group that includes modern birds. Ornithomimid diets have been a matter of some debate—ranging from myrmecophagy (e.g. Russell 1972) to filter-feeding (e.g. Norell et al. 2001)—yet a few recent studies (Barrett 2005; Kobayashi et al. 1999) make a strong argument for a plant-eating habitus.

Ornithomimid skeletal remains, along with those of tyrannosaurs, represent the majority of theropod material recovered from the Kaiparowits Formation, with maniraptorans forming a much less common faunal constituent. Yet, despite their relative abundance, little progress has been made in identifying ornithomimid remains from the formation.

Thirty years ago, an ornithomimid specimen (MNA PI.1762A) consisting of a nearly complete hind limb, fragmentary pelvis, and partial axial column was collected from the Kaiparowits Formation by the Museum of Northern Arizona. This specimen was subsequently referred to the late Maastrichtian taxon *Ornithomimus velox* by DeCourten and Russell (1985). At the time, paly-nomorph evidence supported a Lancian age for the Kaiparowits Formation (Lohrengel 1969) making it coeval with the Denver Formation of Colorado, from which the type specimen of *O. velox* is described (Marsh 1890).

The holotype of *O. velox* is fragmentary, comprised of a distal tibia with astragalus, incomplete left metatarsus, and second pedal digit (YPM 542), together with questionably associated manual elements (YPM 548). Several authors have questioned the validity of this taxon; in their review of Ornithomimidae, Makovicky et al. (2004) noted only a single character as diagnostic for *O. velox*—metacarpal one being the longest in the metacarpus. Unfortunately, *Ornithomimus edmontonicus* also possesses this condition, rendering the trait a synapomorphy of the genus. As Russell (1972) notes, two supposedly diagnostic characteristics

have been derived from the reconstructed metatarsus of *O. velox* provided by Marsh (1890): (1) shortness of the metatarsus; and (2) MT II longer than MT IV (Russell 1972). However, the length and proportion of the metatarsals of *O. velox* can not be determined from the type specimen as there are no definitive contacts preserved between proximal and distal fragments of MCII and IV.

Although the manus is generally considered diagnostic for ornithomimids, no manual elements are preserved with MNA PI.1762A. DeCourten and Russell's (1985) justification for the assignment of the Kaiparowits ornithomimid to *O. velox* lies in pedal ungual morphology (which they identify as similar in both specimens), as well as relative proportions of the pes. Although proportional characteristics have been proposed as diagnostic for individual ornithomimid taxa (Russell 1972), recent studies (e.g., Kobayashi et al. 2006) have challenged the validity of most of these differentiations. Furthermore, while Kobayashi et al. (2006) cite characteristics of the skull, forelimb, and caudal vertebrae as diagnostic for ornithomimids, they do not identify any diagnostic features of the pes among North American taxa. Finally, the specific ratio used by DeCourten and Russell (1985) to assign the Kaiparowits specimen to *O. velox* (ratio of the length of the second pedal ungual to the basal phalanx of digit two) is given by the authors as 0.61-0.64 in "pre-Lancian" North American taxa (*Struthiomimus breveteritus*, *S. currelli*, *S. ingens* [referred to *Ornithomimus edmontonicus* sensu Makovicky et al. 2004], and *S. altus*), 0.78 in MNA PI.1762A, and 0.88 in the holotype of *O. velox*; we do not find this ratio in MNA PI.1762A significantly closer to *O. velox* than to the value given for *O. edmontonicus* and *S. altus*.

An additional argument made by DeCourten and Russell (1985) merits discussion here. Following referral of the Kaiparowits ornithomimid to *O. velox*, DeCourten and Russell (1985) make note of several differences between MNA PI.1762A and *O. edmontonicus*, including a curved pubic shaft and estimated overall body size. In light of these differences, DeCourten and Russell (1985) suggest that *O. edmontonicus* can not be conspecific with *O. velox* and that the referral of *O. edmontonicus*

to the genus *Ornithomimus* should be considered dubious. Removal of the Kaiparowits specimen from the *O. velox* hypodigm renders the argument that *O. edmontonicus* and *O. velox* can not be synonymous on the basis of the additional morphological information provided by that specimen fallible. Thus, the suggestion that *O. velox* may be a senior synonym of *O. edmontonicus* (Makovicky et al. 2004) remains a valid hypothesis.

In sum, we find significant problems with the assignment of MNA PI.1762A to *O. velox* including: (1) the potential synonymy of species in the *Ornithomimus* hypodigm coupled with observed differences between MNA PI.1762A and *O. edmontonicus*; (2) a lack of comparable diagnostic elements between the holotype of *O. velox* and MNA PI.1762A; and (3) the late Campanian age of the Kaiparowits Formation, which negates DeCourten and Russell's (1985) referral of MNA PI.1762A to *O. velox* on the basis of coeval occurrence.

To date, field work conducted by the KBP has added significant morphological data to the discussion of the identity of the Kaiparowits ornithomimid, including associated caudal vertebrae, metatarsal fragments, and phalanges (UMNH VP 12223), two isolated tibiae (UMNH VP 9553) and (UMNH VP 16698), as well as the first articulated forelimb material from the formation. This specimen (UMNH VP 16385) consists of an incomplete and partially crushed manus, carpus, and antebrachium. Additional material recently collected by the Raymond M. Alf Museum (RAM 6794) includes articulated sections of the sacral and caudal axial column, pelvic girdle, and nearly complete right and left hind limbs, which provide a useful comparison to MNA PI.1762A.

Preliminary examination of UMNH VP 16385 reveals similarities to *O. edmontonicus* in the relative size of metacarpal one and in ungual morphology. Additional isolated caudal vertebrae have been collected by the UMNH (UMNH VP 16260; Figure 3A-C, F, and I) and appear most similar to *Dromiceiomimus* (CMN 12228 [*Ornithomimus* sensu Makovicky et al. 2004]; Kobayashi et al. 2006) in general morphology but lack the diagnostic, deeply grooved articulation between pre- and

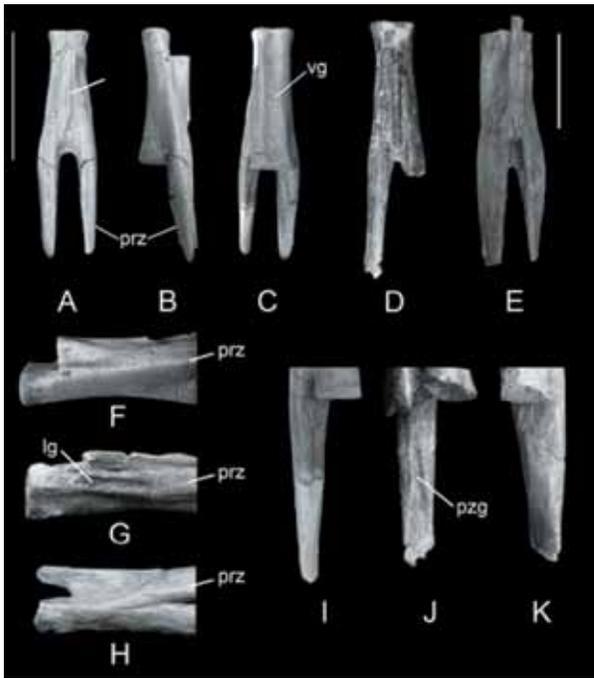


Figure 3. Morphological variation in distal caudal vertebrae of late Campanian ornithomimids from the Western Interior of North America. **A-C, F, and I,** Ornithomimidae incertae sedis from the Kaiparowits Formation (UMNH VP 16260); **D, G, and J,** *Dromiceiomimus breveritus* (CMN 12228, *Ornithomimus edmontonicus* sensu Makovicky et al. 2004; Kobayashi et al. 2006); and **E, H, and K,** *Struthiomimus altus* (CMN 2102/8902). Kaiparowits ornithomimid shown in **A**, dorsal; **B**, right lateral; and **C**, ventral views. Late Campanian ornithomimid caudals in right lateral views, **F, G, and H**, showing the absence of lateral groove for the prezygopophyses in all but *Dromiceiomimus*. Prezygopophyses of ornithomimid caudal vertebrae in ventral views, **I, J, and K**, showing the presence of a ventral groove in *Dromiceiomimus*. **Abbreviations:** **lg**, lateral groove on the centrum caused by articulation with the prezygopophyses; **prz**, prezygopophysis; **pzg**, ventral groove on the prezygopophysis; **vg**, ventral groove on centrum. Upper left scale bar equals 4mm and pertains to views **A-C**. Upper right scale bar equals 5 mm and pertains to **E**. All other views not to scale.

postzygopophyses (Figure 3F-H), as well as the prezygopophyseal ventral groove (Kobayashi et al. 2006; Figure 3I-K). A more comprehensive investigation of ornithomimid materials from the Kaiparowits Formation currently being undertaken by researchers at the UMNH, the Raymond M. Alf Museum, and the College of the Holy Cross is expected to provide additional insights regarding the taxonomic and systematic relationships of North American ornithomimids.

Oviraptorosaurs

Late Cretaceous North American oviraptorosaurs (often referred to as caenagnathids, although this taxonomy is currently contentious) are an endentulous group of medium-sized, feathered maniraptoran dinosaurs possessing keratinous beaks, powerful arms with formidable claws, and often adorned with a cranial fan or crest. While the dietary preference of these unusual dinosaurs is presently unclear, other rarely elucidated aspects of oviraptorosaur paleobiology are known, including many details about egg-laying (Sato et al. 2005) and brooding behavior (Norell et al. 1994; Norell et al. 1995). Although these dinosaurs are remarkably similar to birds in both anatomy and behavior, the predominance of current analyses suggests that these similarities are the result of convergence rather than ancestry (Lu et al. 2004; Makovicky and Sues 1998; Norell et al. 2001; Rauhut 2003; Sues 1997).

Unlike other theropod dinosaurs whose teeth have long been recovered from microvertebrate localities, the toothless condition of oviraptorosaurs prevented their identification in the Kaiparowits until the first diagnostic skeletal material was recovered by UMNH crews in 2002. A nearly complete left manus (missing only the second ungual), carpus, and distal antebrachium (UMNH VP 12765) of a new oviraptorosaur was recovered in articulation within a remnant of channel sandstone (Figure 4) and displays unusual soft tissue preservation. Additional elements—including fragmentary metatarsals and pedal phalanges, and a partial, articulated pedal digit with ungual—were salvaged from the surrounding hillside. The specimen, dubbed *Hagryphus giganteus*, represents the first dinosaur taxon to be named from GSENM and is notably larger than its northern cousins, with an estimated body size increase of 30-40% (Zanno and Sampson 2005). UMNH VP 12765 is also the first North American oviraptorosaur described from south of Montana and South Dakota and represents the southernmost limit yet identified for this enigmatic group of theropods within North America. *Hagryphus* represents the only published account of oviraptorosaurs in the Kaiparowits Formation, and the only unequivocal oviraptorosaur material recovered thus far during the KBP.



Figure 4. Holotype manus of the oviraptorosaur *Hagryphus giganteus* (UMNH VP 12765) in dorsal view. **Abbreviations:** **DI**, digit one; **DII**, digit two; **DIII**, digit three. Scale bar equals 5 cm.

Dromaeosaurs

Dromaeosaurs are among the most commonly recognized dinosaurs. These lethal predators are distinctive in possessing an enlarged “sickle” claw on the second digit of their foot, as well as stiff tails reinforced by dramatically elongated bony struts. Dromaeosaurs are one of the most diverse theropod groups and are considered to be some of the closest cousins to modern birds. A surprising array of miniature, “feathered” species have been

found within exceptionally prolific ancient lake beds in China (Xu et al. 1999; Xu et al. 2000), yet the largest dromaeosaur (*Utahraptor*) is known from Early Cretaceous beds in central Utah (Kirkland et al. 1993).

As a group, dromaeosaurs are known to have been widespread across the late Campanian WIB (Norell and Makovicky 2004). Collection of teeth from microvertebrate localities suggested the presence of “*Dromaeosaurus*” and “velociraptorine” dromaeosaurs in the Kaiparowits Formation over a decade ago (Hutchison et al. 1997). Subsequent collection and detailed examination has verified the existence of at least two dromaeosaur genera in the formation, based on isolated teeth recovered as surface float or within burial sites of herbivorous dinosaurs. In earlier publications (Sampson et al. 2004; Zanno et al. 2005; and Zanno et al. 2005) we provisionally referred these to *c.f. Dromaeosaurus* (Figure 5A) and *c.f. Saurornitholestes* (sensu Sankey 2001; Sankey et al. 2002; Figure 5B), based on comparisons with teeth from the approximately coeval Dinosaur Park and Aguja formations. Although proposals have been put forth supporting the taxonomic utility of tooth morphology in small theropods (Fiorillo and Currie 1994; Smith 2005), these studies have focused either on the intraformational identification of small theropod teeth (which can be compared to teeth associated with diagnostic skeletal materials) or on intraspecific variation in tooth morphology. Thus far, interformational and interspecific diagnostic utility have not been considered. We are unaware of any published study demonstrating that isolated dromaeosaur teeth are referable at the genus or species level; in fact, Farlow et al. (1991) demonstrated significant overlap in morphological parameters of isolated dromaeosaur teeth from different genera, and Currie and Varricchio (2004) noted that the teeth of *Saurornitholestes* are similar to those of the younger dromaeosaur *Atrociraptor* from the Horseshoe Canyon Formation. Additionally, nearly all other dinosaurs currently known from the Kaiparowits Formation represent new species or genera, including tyrannosaurs, ceratopsians, hadrosaurs, and oviraptorosaurs. Thus we regard it as unlikely that the as-yet-undescribed small-bodied theropods inhabiting the Kaiparowits ecosystem would be an exception to this pattern.

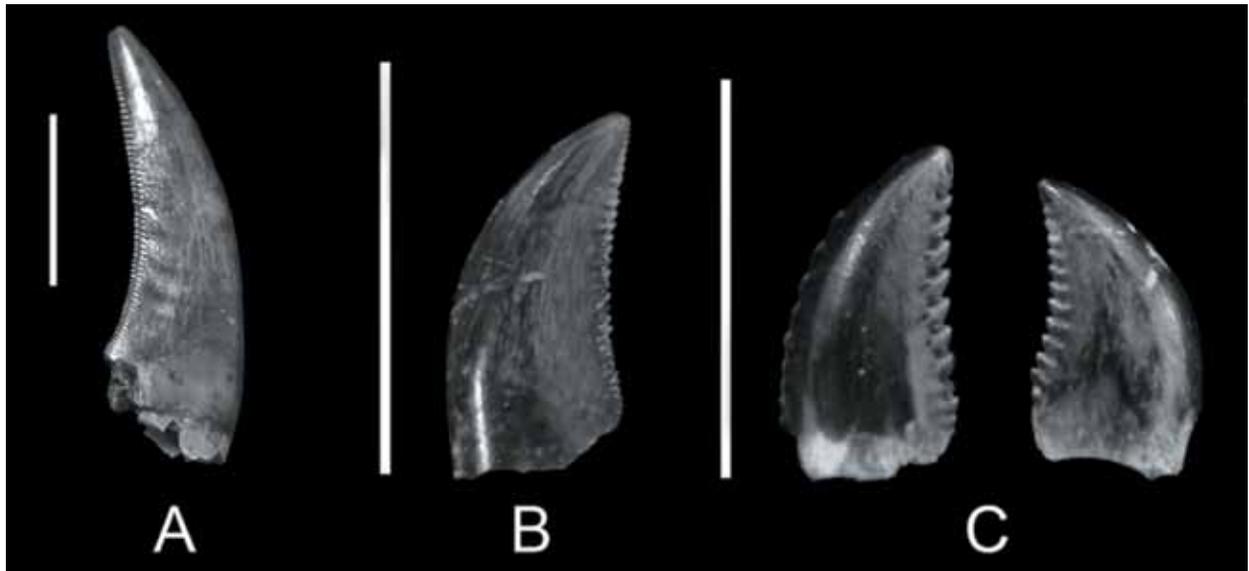


Figure 5. Maniraptoran theropod teeth from the Kaiparowits Formation. **A**, *Dromaeosaurus*-type (UMNH VP 16306); **B**, *Saurornitholestes*-type (UMNH VP 11803); and **C**, troodontid (UMNH VP 12507). Scale bar equals 1 mm.

Given this documented pattern of latitudinal diversity, we support a more conservative approach, instead of referring isolated teeth to known WIB genera, we identify these teeth either as “*Dromaeosaurus*-type” and “*Saurornitholestes*-type”.

Postcranial materials potentially referable to Dromaeosauridae include isolated pedal phalanges and unguals. However, other than a pedal phalanx, similar to *Saurornitholestes* (PII-I; UMNH VP 12494), these elements have not yet proven to be taxonomically useful. The most complete dromaeosaur material thus far discovered was collected by Howard Hutchison of the University of California at Berkeley’s Museum of Paleontology in 1994. The specimen, UCMP 149171, consists of a proximal tibia, fragmentary metatarsals, pedal phalanges, and pedal unguals, as well as some fragmentary skull material, including the basioccipital, fused parietals, and portions of the squamosals. Preliminary examination reveals differences between this specimen and northern dromaeosaurs; however, additional study is needed before it can be determined if this poorly preserved specimen represents a new taxon.

Troodontids

Troodontids are an enigmatic group of feathered maniraptoran dinosaurs, notable for exhibiting some of the smallest body sizes and the largest

relative brain sizes within Dinosauria. Only a single genus is currently recognized in North America—*Troodon* (Currie 1987a). As a result of their distinctive teeth, some authors have proposed an omnivorous diet for these theropods (Holtz 1998); however, carnivory is still the most widely regarded hypothesis for the diet of troodontids.

Previously, the presence of *Troodon* in the Kaiparowits Formation was documented entirely on the basis of isolated teeth, which are widely recognized as diagnostic for the only North American member of the group (Currie 1987a; Makovicky and Norell 2004). However, given that only a single species of troodontid is known from the Late Cretaceous WIB, it is unclear whether North American troodontid teeth are diagnostic at the genus or species level. Over half a dozen troodontid teeth have been collected by UMNH crews since 2000 (Figure 5C), adding to the numerous additional teeth collected during earlier microvertebrate surveys (Eaton et al. 1999; Hutchison et al. 1997).

During the 2005 field season, an exceptionally well preserved, isolated left frontal (UMNH VP 16303) was discovered in the Kaiparowits Formation (Figure 6A). The frontal compares closely with that of *Troodon formosus* (CMN 12340; Fig 6B), known from the contemporaneous Dinosaur Park Formation in Alberta, in possessing an elon-

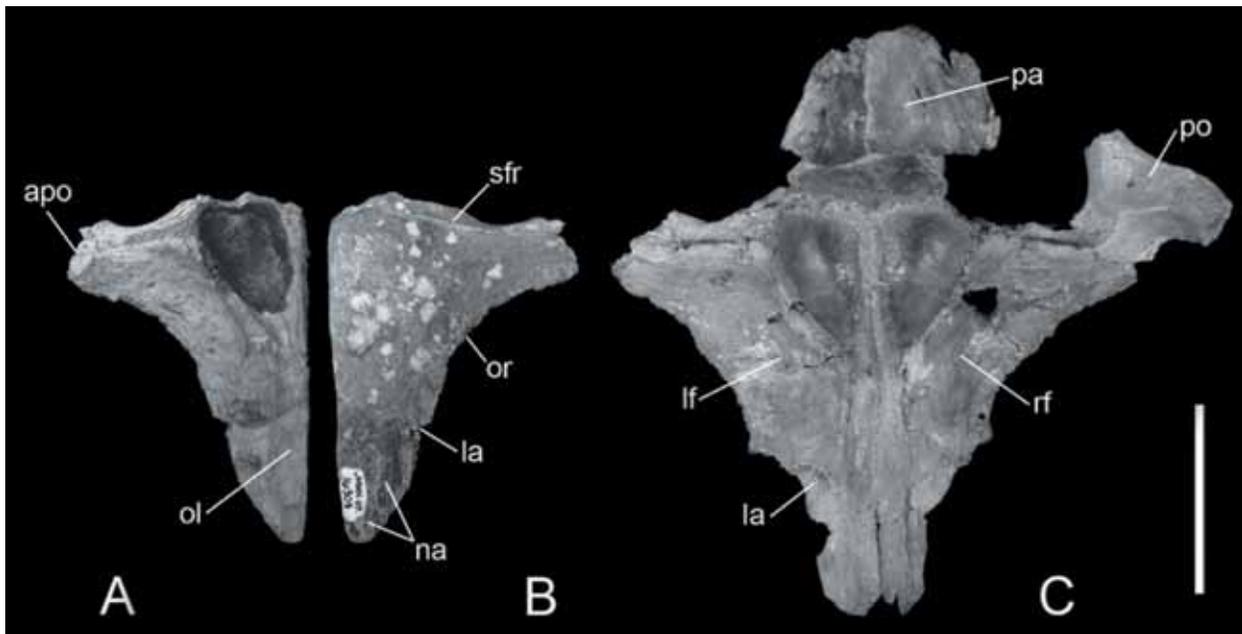


Figure 6. Morphology of troodontid frontals from the late Campanian of the Western Interior of North America. A-B UMNH VP 16303, troodontid incertae cedis from the Kaiparowits Formation of Utah in **A**, ventral; and **B**, dorsal views; **C**, CMN 12340, *Troodon formosus* cranium from the Dinosaur Park Formation, Alberta, Canada in ventral view. **Abbreviations:** apo, articular surface for the post orbital; la, articular surface for the lacrimal; lf, left frontal; na, articular surface for the nasal; ol, olfactory lobe; or, orbital margin; pa, parietal; po, postorbital; rf, right frontal; sfr, ridge on the rostral margin of the supratemporal fenestra. Scale bar equals 4 cm.

gate, triangular morphology, a extensive orbital rim, a prominent ridge defining the rostral limit of the supratemporal fenestra, and a large, laterally extensive post orbital process. However, the Kaiparowits specimen differs significantly from the Dinosaur Park specimen in a number of features including: absence of medial depression caudal to nasal contact; weakly excavated lacrimal suture on frontal; and lack of ventral overlap of the lacrimal onto the frontal. As a result of this diagnostic element, we can confidently identify a troodontid closely related to, yet likely distinct from, *Troodon formosus* in the Kaiparowits Formation.

As mentioned, additional isolated “deinonychosaurian” material, including pedal phalanges, unguals, and caudal vertebrae, have been collected by the UMNH and may be referable to this taxon. However, much of this material is damaged and more research is needed to differentiate between isolated elements referable to troodontids versus the two (at minimum) poorly known dromaeosaurs in the formation.

Aves

Today, abundant evidence exists in support of the hypothesis that birds are the direct descendants of maniraptoran theropod dinosaurs, and thus are to be considered dinosaurs themselves. Just as modern birds exist as one of the most diverse vertebrate groups alive today, birds are also known to have had a strong representation during the Cretaceous.

To date, a number of fragmentary avian skeletal elements have been collected during the KBP. However, thus far, the only avian taxon diagnosed from the Kaiparowits is *Avisaurus* (Hutchison 1993). Two species of *Avisaurus* are known from Late Cretaceous formations in Montana, *A. archibaldi* (Brett-Surman and Paul 1985) from the Hell Creek Formation (also known from the Lecho Formation in Argentina) and *A. gloriae* (Varricchio and Chiappe 1995) from the Upper Two Medicine Formation. Both are known solely from the tibiotarsus. By comparison, the Kaiparowits specimen represents one of the most complete Late Cretaceous enantiornithine birds, preserving a large portion of the skeleton including: partial axial column

with pygostyle, well developed pectoral girdle and forelimb with a robust keel, U-shaped furcula, and papillae remigiales, and robust tarsometatarsus with highly recurved unguals (Hutchison 1993). Preliminary study by Hutchison (1993) indicates that this specimen represents a new species of *Avisaurus*, but following publication of an abstract describing the find, no subsequent research has been undertaken to name the specimen; it therefore remains *Avisaurus* sp.

Discussion

Nearly all Late Cretaceous theropod clades known to have inhabited North America can now be documented in the Kaiparowits Formation, including tyrannosaurids, ornithomimids, oviraptorosaurs, “dromaeosaurine” and “velociraptorine” dromaeosaurs, troodontids, and avians. Notably absent are therizinosaurs, a rare theropod clade, whose presence in the Campanian of North America is suggested from a single specimen recovered from the Dinosaur Park Formation in Alberta (Currie 1987b).

Recent radiometric dates derived from several bentonite horizons within the Kaiparowits establish the formation as coeval with fossiliferous portions of the Dinosaur Park, upper Judith River, and upper Two Medicine formations (Roberts et al. 2005). As such, the ecological diversity preserved in the Kaiparowits offers important insight into the phylogeny and biogeographic patterns of theropod dinosaurs within the WIB during the Late Cretaceous. Results of the KBP demonstrate that all major groups of theropod dinosaurs known from northern late Campanian formations contributed to the Kaiparowits ecosystem (Zanno 2005). Yet, despite the apparent ecological homogeneity among theropod groups within late Campanian WIB formations, theropod species appear to be highly endemic. During the KBP enough diagnostic material has been collected to verify that the Kaiparowits tyrannosaur and oviraptorosaur are local endemics. A potentially diagnostic troodontid frontal (UMNH VP 16303) is different enough from *Troodon formosus* to currently prevent its assignment to the northern troodontid. Similarly, the

most complete dromaeosaurid specimen collected thus far from the Kaiparowits Formation (UCMP 149171) shows substantial differences relative to those species known to have inhabited northern WIB ecosystems. Thus, only a single theropod taxon from the Kaiparowits Formation is presently referred to an existing WIB genus—*Avisaurus*—and no formal study of this specimen has been conducted confirming this assignment.

Paleoenvironmental interpretations of upper Campanian WIB formations suggest a span of habitats, from wet alluvial to arid coastal plain settings. Yet this substantial environmental variation appears to have had little effect upon the presence of various theropod groups within the basin (although they may be affecting local endemism and speciation patterns). Rather than determining the diversity of theropods, paleoenvironmental conditions may have impacted the relative abundance of these clades within WIB formations, especially if the formations are sampling different primary habitat. Preliminary evidence seems to support this hypothesis, as tyrannosaurs (*Gorgosaurus*), and paravians (*Saurornitholestes* and *Troodon*) appear to be the most abundant theropods in the Dinosaur Park Formation (Currie 1987b), whereas tyrannosaurs and ornithomimids are the most commonly recovered theropods in the Kaiparowits Formation. Although we recognize that variable taphonomic factors can result in differential preservation of organisms thereby producing a difference in relative abundance values, we see no vast differences between the skeletons of Kaiparowits ornithomimids, oviraptorosaurs, and North American troodontids that would be expected to produce such biases and the former is clearly the most abundant theropod clade in the Kaiparowits Formation. While the smaller-bodied dromaeosaurs and avians may have a poorer representation in the Kaiparowits due to preservational or collection biases (small skeletons are harder to find), and the reverse conditions are undoubtedly impacting tyrannosaur abundance data, the sedimentology of the Kaiparowits and Dinosaur Park formations are sufficiently similar that invoking preservational biases as the sole explanation in this instance is likely not warranted. Ultimately, while we find these patterns of interest, a larger sample size and greater taphonomic control is needed to determine if these differences are

indeed reflections of variation in regional ecology, or simply the result of skewed sampling.

Conclusions

The Kaiparowits Basin Project, spearheaded by the UMNH and the University of Utah, is currently making significant contributions to our understanding of the theropod dinosaur fauna of the Kaiparowits Formation, as well as to the taxonomy, biogeography, and phylogeny of the theropod clades that inhabited the WIB during the late Campanian. To date, the project has resulted in identification of three new theropod taxa: (1) *Hagryphus giganteus*, the first conclusive southern Cretaceous oviraptorosaur, and the first dinosaur to be named from GSENM; (2) an unnamed tyrannosaur genus, based upon a largely complete juvenile specimen; and (3) the first identifiable troodontid cranial material from the monument, which possesses a significant degree of morphological disparity from the northern *Troodon formosus*. Reinvestigation of a partial ornithomimid hindlimb and pelvis raises considerable questions about its referral to the Maastrichtian species *Ornithomimus velox*, while research in progress on the first diagnostic ornithomimid forelimb material confirms a close relationship between the Kaiparowits ornithomimid and the genus *Ornithomimus*.

Comparison of the newly revealed Kaiparowits theropod fauna with coeval late Campanian formations within the WIB demonstrates a surprising amount of homogeneity in theropod taxa at the clade (“family”) level, particularly given the perceived variation in paleoenvironment between investigated formations. Yet the data also establishes a high degree of local endemism at the genus and species levels. As a result we hypothesize that variation in paleoenvironment may be better expressed through relative abundance rather than presence/absence data for theropod clades within the WIB.

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