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# First occurrence of a tyrannosaurid dinosaur from the Mesaverde Group (Neslen Formation) of Utah: Implications for upper Campanian Laramidian biogeography

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ABSTRACT

Although upper Campanian dinosaur assemblages are well-known from Alberta, Montana, southern Utah, and New Mexico, specimens from Wyoming and central and eastern Utah are very rare. This area constitutes a biogeographic break between northern and southern biogeographic provinces, so any specimens from this region are critical to understanding the origin, evolution, and limits of upper Campanian biogeographic zones on the west margin of the Western Interior Seaway. We report the discovery of a theropod dinosaur partial hindlimb from the Book Cliffs area northeast of Green River, Utah. The specimen was recovered from the Palisade coal zone in the Neslen Formation (Mesaverde Group), which is dated to the mid-Campanian based on ammonite biostratigraphy and radioisotopic age constraints. The specimen, comprising a partial fibula, the distal half of metatarsal II, a complete metatarsal IV, and a partial metatarsal V, can be assigned to Tyrannosauridae based on a number of synapomorphies, including a bipartite iliofibularis tubercle on the fibula and a teardrop shaped articular surface for metatarsal III on the medial surface of the distal portion of metatarsal IV. This is the first unambiguous tyrannosaurid dinosaur reported from the Mesaverde Group and represents an important biogeographic record situated between northern and southern upper Campanian vertebrate assemblages. Specifically, we identify morphological evidence on the pes that separates northern (Montana and Alberta) and southern (southern Utah and New Mexico) tyrannosaurid dinosaurs, and suggests that the Book Cliffs specimen belongs to the northern group. This implies that either the biogeographic boundary between the northern and southern Campanian assemblages lies somewhere between central and southern Utah or that the Book Cliffs taxon represents a northern emigrant in the southern assemblage.


## 1. Introduction

Extensive prospecting and active collecting in Late Cretaceous strata of western North America have discovered numerous specimens, both marine and terrestrial. Campanian deposits are especially well-sampled on a continental scale with fossiliferous units ranging from Mexico to Alaska. These deposits were laid down along the eastern margin of a north-south oriented land mass called Laramidia. The Western Interior Seaway (WIS) effectively isolated Laramidia from eastern North America (Russell, 1995; Roberts and Kirschbaum, 1995; Hay et al., 1999) with periodic connections to Asia via Beringia depending on global sea level (e.g., Haq et al., 1987; Miller et al., 2005). This isolation combined with excellent sampling of the paleobiota makes the Campanian assemblages of Laramidia well-suited for large-scale paleobiogeographical analyses.

Work by Lehman (1997, 2001) suggested evidence for a high degree of latitudinal provincialism with two mostly distinct, but slightly overlapping northern and southern provinces. Although his findings were supported by evidence from pollen, plant macrofossils, and marine organisms, the lack of stratigraphic control and small taxonomic sample size led to criticisms by Sullivan (2003) and Sullivan and Lucas (2003, 2006). Recently, Gates et al. (2010) built upon Lehman's work by more than doubling the taxonomic sample, adding an additional fossil-bearing formation, increasing the chronostratigraphic control, and applying four separate statistical analyses to the biogeographic data. These results supported Lehman's hypothesis of northern and southern provinces but left the nature of the intervening region unclear. Gates et al. (2010) suggest that this ecotone either displayed semi-isolated regional faunas with a large zone of overlap or a continuous latitudinal diversity gradient throughout Laramidia.

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One dinosaur clade that shows a distribution initially restricted to Laramidia is the tyrannosaurid theropod dinosaurs (Tyrannosauridae), which are known from throughout western North America during the Campanian (Holtz, 2004; Brusatte et al., 2010; Carr et al., 2011). Tyrannosaurids belong to a larger coelurosaurian theropod clade called Tyrannosauroidea, defined as the clade comprising *Tyrannosaurus rex* and all taxa sharing a more recent common ancestor with *T. rex* than with birds (Holtz, 2004). Not only does this clade include the large-bodied, derived forms such as tyrannosaurids, but also more basal small-bodied taxa from the Middle Jurassic onward (e.g., *Proceratosaurus bradleyi* from the Middle Jurassic [Rauhut et al., 2010], *Guanlong wucaii* [Xu et al., 2006], *Stokesosaurus clevelandi* [Madsen, 1974], and *Juratyrant langhami* [Benson, 2008; Brusatte and Benson, 2013] from the Late Jurassic, *Eotyrannus lengi* [Hutt et al., 2001], *Dilong paradoxus* [Xu et al., 2004], and *Xiongguanlong baimoensis* [Li et al., 2010] from the Early Cretaceous, and *Dryptosaurus aquilunguis* [Cope, 1866] from the latest Cretaceous). Tyrannosauroids are found throughout North America, Asia, Europe, and possibly Australia (Benson et al., 2010). The more-derived, large-bodied clade Tyrannosauridae is confined to western North America and Asia and is only known from Campanian–Maastrichtian (Late Cretaceous) strata.

Asian tyrannosauroid taxa comprise some basal forms (e.g. *Guanlong* and *Dilong*) as well as more derived Maastrichtian taxa belonging to Tyrannosauridae (e.g., *Alioramus remotus* Kurzanov, 1976, *A. altai* [Brusatte et al., 2009], *Tarbosaurus bataar* [Maleev, 1955], and *Zhuchengtyrannus magnus* [Hone et al., 2011]). North American tyrannosauroids are mostly represented by Campanian-aged taxa from Laramidia belonging to Tyrannosauridae. *Appalachiosaurus montgomeriensis* from Alabama in eastern North America (Carr et al., 2005) and *Stokesosaurus clevelandi* from Utah in western North America have been placed outside Tyrannosauridae but within Tyrannosauroidea by recent phylogenies (e.g., Carr et al., 2005; Carr and Williamson, 2010; Brusatte et al., 2010; Carr et al., 2011).

Tyrannosaurid taxa recovered from northern Laramidian strata include species such as *Gorgosaurus libratus* Lambe, 1914, *Albertosaurus sarcophagus* Osborn, 1905, and several species of *Daspletosaurus*. Two southern Laramidian species were recently described, *Bistahieversor sealeyi* from New Mexico (Carr and Williamson, 2010), and *Teratophoneus curriei* from the Kaiparowits Formation of southern Utah (Carr et al., 2011), along with a complete fourth metatarsal from the 'El Gallo' Formation in Mexico (Peecook et al., 2010, in press) and a new undescribed taxon from the older Wahweap Formation of southern Utah (Loewen et al., 2010; in review). Younger Maastrichtian strata from North America have produced widespread occurrences of *Tyrannosaurus rex* (e.g., Osborn, 1905; Brochu, 2002; Carr and Williamson, 2004; Sampson and Loewen, 2005) and the basal tyrannosauroid *Dryptosaurus aquilunguis* from eastern North America (Cope, 1866; Carpenter et al., 1997; Brusatte et al., 2011). Because tyrannosaurids are taxonomically diverse, distributed throughout Laramidia during the Campanian, and individual taxa are restricted to small geographic regions, they provide important data for testing hypotheses about biotic provinciality and endemism in western North America during this time period.

Dinosaur fossil occurrences from the Neslen Formation (Mesaverde Group) of central eastern Utah represent key biogeographic records situated between southern coeval middle Campanian strata in the Kaiparowits (southern Utah) and San Juan (New Mexico) basins, and equivalent northern strata in Montana and Alberta. Here we report the first occurrence of a tyrannosaurid dinosaur from the Neslen Formation. Tyrannosaurids from the Late Cretaceous of Utah represent important biogeographic occurrences of this group within North America because they provide insights into the timing and position of possible paleogeographic barriers, and they bridge the gap between previously described northern and southern taxa. The only other dinosaur remains reported from the Neslen Formation are a partial hadrosaurid skeleton with associated integument impressions (BYU 13258; Anderson et al., 1999; Gates et al., 2009). Preliminary phylogenetic study places this specimen within the Hadrosaurinae (=Saurolophinae), and suggests that it is most closely related to *Gryposaurus* (Gates et al., 2009).

*Institutional Abbreviations*. AMNH, American Museum of Natural History, New York, New York, U.S.A.; BHI, Black Hills Institute, Hill City, South Dakota, U.S.A.; BYU, Brigham Young University, Provo, Utah, U.S.A.; IGM, Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, México; NMC, National Museum of Canada; NMMNH, New Mexico Museum of Natural History & Science, Albuquerque, New Mexico, U.S.A.; RMM, Red Mountain Museum, Birmingham, Alabama, U.S.A.; TCM, The Children's Museum of Indianapolis, Indianapolis, Indiana, U.S.A.; TMP, Tyrell Museum of Paleontology, Drumheller, Alberta, Canada; and UMNH, Natural History Museum of Utah (formerly Utah Museum of Natural History), Salt Lake City, Utah, U.S.A.

## 2. Geologic setting

The upper Campanian paleogeography of Utah featured western highlands formed by thrusting during the Sevier Orogeny with a broad foreland basin to the east (e.g., Roberts and Kirschbaum, 1995; Hintze and Kowallis, 2009). This basin was filled by an epicontinental seaway extending from the Gulf of Mexico northward to the Arctic Ocean known as the Western Interior Seaway (WIS), dividing North America into two landmasses, Appalachia to the east and Laramidia to the west (Williams and Stelck, 1975; Roberts and Kirschbaum, 1995). During the upper Campanian, the paleoshoreline of the WIS fluctuated between central Utah and western Colorado (Roberts and Kirschbaum, 1995). In southern Utah, the Kaiparowits Formation was deposited as a prograding clastic wedge within the rapidly subsiding foreland basin east of the Sevier Orogenic Belt. This unit is interpreted to have been deposited on a warm, subhumid, low-relief alluvial plain with periodic aridity. High sedimentation rates precluded the formation of coal beds within this formation (Roberts, 2007).

In eastern Utah, western Colorado, and western Wyoming, a thick package of nearshore, lagunal, estuarine, and coastal fluvial strata were deposited, collectively known as the Mesaverde Group (Hettinger and Kirschbaum, 2002). In the area around Green River, Utah the Mesaverde Group comprises the Blackhawk Formation, Buck Tongue of the Mancos Shale, Sego Sandstone, Neslen Formation, Bluecastle Tongue of the Castlegate Sandstone, and Farrer Formation (Hettinger and Kirschbaum, 2002). The specimen described here was discovered in the Neslen Formation, which consists of mudstones, siltstones, sandstones, and coals, with an average thickness of ~100 m in the area (Willis, 1986). It crops out along the Book Cliffs which run through eastern Utah from Price south to Green River and then eastward into Colorado (Fig. 1). The unit is interpreted as tidally influenced fluvial and coastal-plain sediments deposited along the western margin of the WIS (Franczyk et al., 1990). Occurrences of abundant *Teredolites* wood borings reported from the lower Neslen Formation (Anderson et al., 1999) can be interpreted as indicating some degree of marine influence (Kelly and Bromley, 1984).

The Book Cliffs specimen (UMNH VP 16395) was collected from the Palisade coal zone, the lowest coal zone within the lower Neslen Formation, just above the basal contact with the Sego Sandstone (Fig. 2). This stratigraphic position is similar to that of a previously reported hadrosaurine skeleton (Anderson et al., 1999; Gates et al., 2009). Interfingering ammonite-bearing marine units