

A tyrannosaurid pedal ungual from the Williams Fork Formation (Campanian) of Colorado and its implications for the biogeography of Laramidian dinosaurs

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ABSTRACT:

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A right theropod pedal ungual phalanx II-3 from the Campanian Williams Fork Formation of northwestern Colorado is described, and a combination of features, including the large size, tapering distal tip, robust and stout overall form, triangular cross-section, and a relatively flat ventral surface allows a confident referral to Tyrannosauridae Osborn, 1906. Although this specimen was found in a relatively southern state, the proximal articular surface of this ungual is similar to that of *Gorgosaurus libratus* Lambe, 1914, a taxon found in the northern state, Alberta. Although based on limited evidence, this may suggest that the range of tyrannosaurids considered endemic to the north of Laramidia extended farther south than previously thought.

Key words: Dinosauria; Theropoda; Tyrannosauridae; Fossil record; Pedal ungual anatomy; Dinosaur biogeography.

INTRODUCTION

Tyrannosauridae Osborn, 1906 is a clade of large-bodied theropod dinosaurs that are characterized by their deep, massive skull with robust teeth, remarkably short forelimbs with only two functional digits, and proportionally elongated and gracile hindlimbs that indicate enhanced cursorial ability (Currie 2003; Holtz 2004; Carr *et al.* 2017). These carnivorous dinosaurs reigned as the apex predators of western North America (Laramidia) and Asia during the Campanian and Maastrichtian stages of the Cretaceous Period (Holtz 2004; Brusatte and Carr 2016). During the Campanian, Tyrannosauridae had a remarkable diversity in Laramidia, and are represented by an exceptionally rich fossil record that includes nearly complete skulls and skeletons from numerous localities in provinces and states such as Alberta, Montana, New Mexico and southern Utah

(Currie 2003; Carr and Williamson 2010; Carr *et al.* 2011, 2017; Loewen *et al.* 2013; Voris *et al.* 2020, 2022). This is different from the pattern of the fossil record of the Maastrichtian Stage, although in part this may be due to bias in the fossil record (Voris *et al.* 2020). In the Laramidia fossil record of early Maastrichtian age, only two species, *Albertosaurus sarcophagus* Osborn, 1905 and *Nanuqsaurus hoglundi* Fiorillo and Tykoski, 2014, have been reported (Bell and Currie 2014; Fiorillo and Tykoski 2014). In the late Maastrichtian fossil record of western North America, only the largest type of tyrannosaurid, *Tyrannosaurus rex* Osborn, 1905, is found (Carr and Williamson 2004; Brusatte and Carr 2016).

Although the tyrannosaurid fossil record of Campanian-age localities of western North America is very rich, it is mostly biased toward the relatively northern and southern regions (e.g., Carr *et al.* 2011; Voris *et al.* 2020). In fact, it is not only biased towards

tyrannosaurids, and, although many other types of dinosaurs had high species diversity in Laramidia during the Campanian period, the fossil record is also mostly biased towards places such as Alberta, Montana, New Mexico, and southern Utah (e.g., Longrich *et al.* 2013; Thomson *et al.* 2013; Longrich 2014). Such phenomena suggest that some degree of north-south provinciality was present within Campanian dinosaurs in Laramidia (e.g., Lehman 1987; Sampson *et al.* 2010; Longrich 2014; Bell *et al.* 2015; Dalman *et al.* 2022) but it is still debatable whether there were latitudinal gradients between northern and southern faunas (Longrich 2014; Lucas *et al.* 2016; Voris *et al.* 2020). Partly, this is because of the very rare nature of Campanian dinosaur fossils from areas such as Colorado, Wyoming, and central and eastern Utah that represent components of the faunas that were located between northern and southern assemblages of Laramidia (Thomson *et al.* 2013; Foster and Hunt-Foster 2015).

The Campanian Williams Fork Formation of northwestern Colorado has produced numerous fossils, including freshwater mollusks, pollen and plant macrofossils, and vertebrate microfossils (e.g., Foster and Hunt-Foster 2015). Unfortunately, the dinosaur fossils that have been recovered from the formation are often undescribed or extremely fragmentary. So far, only one partial ceratopsid skull (SDNHM 43470) and fragmentary dinosaur teeth have been described in formal peer-reviewed literature (Diem and Archibald 2005; Brand *et al.* 2022), in which the former is generally considered as a *Pentaceratops*-like taxon (e.g., Longrich 2014; Fowler and Freedman Fowler 2020). Brand *et al.* (2022) described several fragmentary dinosaur teeth that were collected from the Williams Fork Formation locality (J&M site), and assigned them to an indeterminate dromaeosaurid, cf. *Richardoestesia* sp., and indeterminate hadrosaurids. An unpublished master's thesis by Diem (1999) described many more fragmentary dinosaur fossils from the Williams Fork Formation, and even assigned some of them to particular taxa (e.g., *Ankylosaurus magniventris* Brown, 1908). Such assignments were criticized by Sullivan and Lucas (2006), who noted that such referrals are based on very limited material and/or are inconsistent with recognized temporal distributions. Thus, Sullivan and Lucas (2006) treated most of the assignments made by Diem (1999) as doubtful and concluded that most of the dinosaur fossils from the formation are not identifiable beyond 'family' level. Nevertheless, descriptions of any additional dinosaurian material from the formation would be important in further characterizing the scarcely known dinosaurian fauna of the Williams Fork Formation.

In this work, a pedal ungual phalanx of a tyrannosaurid theropod from the Williams Fork Formation is described. While this specimen (UCM 87636) was briefly described by Diem (1999), the obvious lack of information about the dinosaur fauna of the Williams Fork Formation encourages the description of the specimen here in formal, peer-reviewed literature. Furthermore, a significant amount of new information about tyrannosaurid skeletal anatomy has become available within the last decade, which enables comparisons that were not available to Diem (1999). While obviously based on limited evidence, UCM 87636 is unique in exhibiting a character that is similar to the northern Laramidian taxon *Gorgosaurus libratus* Lambe, 1914. This provides an opportunity to test the hypothesis about high levels of endemism among Campanian dinosaurs of western North America, including tyrannosaurids.

GEOLOGICAL SETTING

The Upper Cretaceous Williams Fork Formation is exposed in northwestern Colorado, and is primarily composed of coastal plain deposits (e.g., Foster and Hunt-Foster 2015; Fowler 2017). While the thickness of the formation varies regionally (e.g., Fowler 2017), the thickest parts are more than 1000 m (e.g., Foster and Hunt-Foster 2015; Fowler 2017). In the southern Piceance Basin of Colorado, the Williams Fork Formation is the uppermost part of the 'Mesaverde Group', and overlies the Iles Formation within the Group (Foster and Hunt-Foster 2015).

UCM 87636 was discovered at UCM Locality 99010 in the Piceance Basin, Rio Blanco County of Colorado. Although no information exists other than that this locality is located at the Williams Fork Formation in the museum record (J. Van Veldhuizen, pers. comm., September 2021), a field crew that participated in the excavation of the UCM Locality 99010 has reported that the site is likely to be in the lower half of the middle third of the formation (J. Foster, pers. comm., January 2022). The ammonite *Didymoceras cheyennense* Meek and Hayden, 1856 (74.60–74.21 Ma) occurs in the lower part of the Williams Fork Formation (e.g., Fowler 2017), and Diem and Archibald (2005) correlated the upper boundary of the formation to the basalmost Maastrichtian *Baculites baculus* ammonite Zone (72.05 Ma) based on occurrences of pollen that are similar to those in the Fox Hills Formation and the lower part of the Lance Formation. Brownfield and Johnson (2008) reported a K/Ar age of 72.5 ± 5.1 Ma

from the Yampa bed of the lowermost part of the Williams Fork Formation, but Fowler (2017) noted that the large analytical error (± 5.1 Ma) still permits it to reside within the *Didymoceras cheyennense* Zone. More recently, Walker *et al.* (2021) reported a U/Pb age of 74.52 ± 0.11 Ma and a sanidine $^{40}\text{Ar}/^{39}\text{Ar}$ age of 73.10 ± 0.12 Ma for the Coal Canyon ash of the lower Williams Fork Formation, which they interpreted as coeval to the Yampa bed. Walker *et al.* (2021) noted that the result of $^{40}\text{Ar}/^{39}\text{Ar}$ sanidine analyses is preferable as this is based on higher precision analyses, and suggested the Coal Canyon ash may correlate with the *Baculites reesidei* ammonite Zone (72.94 ± 0.45 Ma). These data suggest the vertebrate fauna of the Williams Fork Formation, including the tyrannosaurid taxon represented by UCM 87636, likely dates to the latest Campanian. Of note, Brand *et al.* (2022) suggested a Judithian–Lancian age, i.e., sometime between the late Campanian and the late Maastrichtian for the age of a locality (J&M site) that is located at the upper portion of the lower half of the Williams Fork Formation. These hypotheses are based on mammalian fossils and those of the squamate *Peneteius* Estes, 1969 and the ray *Myledaphus* Cope, 1876, respectively (Brand *et al.* 2022).

While mostly represented by fragmentary remains, the Williams Fork Formation contains a diverse vertebrate fauna that consists of fishes, amphibians, squamates, turtles, champsosaurs, crocodyliforms, dinosaurs and mammals (Diem 1999; Sullivan and Lucas 2006; Foster and Hunt-Foster 2015). The dinosaur fauna includes ankylosaurs, ceratopsians, hadrosaurids, thescelosaurids, tyrannosaurids, dromaeosaurids and troodontids, but very few of them have been described in peer-reviewed literature (Diem 1999; Sullivan and Lucas 2006; Foster and Hunt-Foster 2015; Brand *et al.* 2022).

MATERIAL AND METHODS

Due to lack of funding at the beginning of this project, this study had to be conducted using a high-quality cast of the original specimen housed at the Fossil Vertebrate Collection at the University of Colorado Boulder Museum of Natural History (UCM 87636) made through 3D scanning. To reconstruct the complete ungual to estimate the complete length and the internal angle, the two-circle method of Fowler *et al.* (2009) was used. The reconstructed internal angle and complete lengths were measured through the program ImageJ (Schneider *et al.* 2012). Comparisons with other theropods were made through an extensive

review of the literature. The anatomical nomenclature used in this study follows Brochu (2003), Carr (2005), Carr *et al.* (2005) and Funston *et al.* (2021).

Institutional abbreviations

SDNHM – San Diego Natural History Museum, California, USA; UCM – The Fossil Vertebrate Collection at the University of Colorado Boulder Museum of Natural History, Colorado, USA.

SYSTEMATIC PALEONTOLOGY

Tyrannosauroida Osborn, 1906

Tyrannosauridae Osborn, 1906

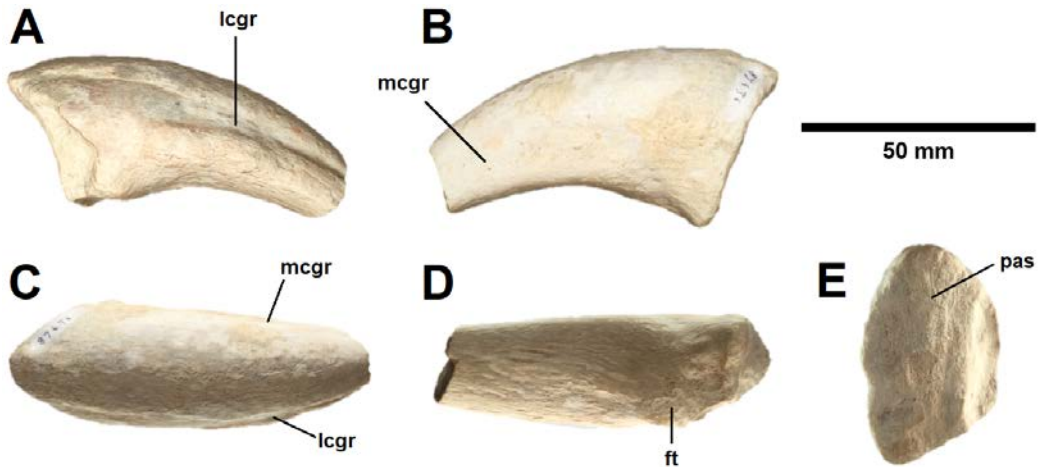
Tyrannosauridae indet.

(Text-figs 1, 2)

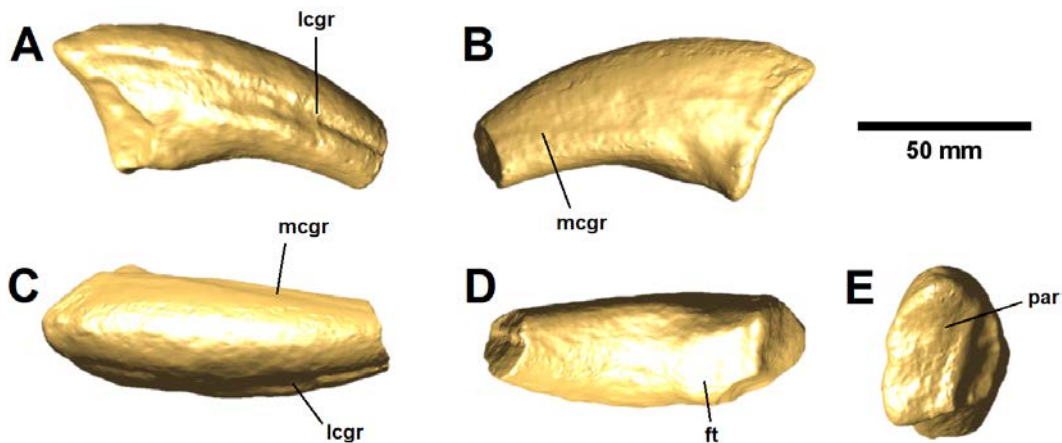
MATERIAL: UCM 87636 (partial right pedal ungual II-3).

REMARKS: While Diem (1999) did refer this specimen to the Tyrannosauridae, no evidence for this assignment was given other than that Philip J. Currie told J. David Archibald in a personal communication that this specimen belongs to this clade. Thus, discussion of the assignment of UCM 87636 to Tyrannosauridae is briefly justified here. The combination of the large size, the tapering distal portion, the stout and robust nature, triangular cross-section, and flat ventral surface with a relatively gentle curvature compares favorably to large theropod pedal unguals (e.g., Lambe 1917; Brochu 2003; Holtz 2004; Lehman and Wick 2013; Funston *et al.* 2021). While a gigantic crocodyliform that would have been large enough to have had similarly-sized unguals was reported from the Williams Fork Formation (Foster and Hunt-Foster 2015), crocodyliform unguals tend to be elongated, dorsoventrally flattened, bear a prominent lip at their proximodorsal position, and have little curvature at their ventral surface (e.g., Novas *et al.* 2005). Given that UCM 87636 is nearly identical to described examples of tyrannosaurid pedal unguals (e.g., Lambe 1917; Brochu 2003; Holtz 2004; Lehman and Wick 2013; Mallon *et al.* 2020), this specimen is unlikely to pertain to a giant crocodyliform.

Among theropods found in the Campanian–Maastrichtian strata of Laramidia, only caenagnathids (e.g., Xu *et al.* 2007), ornithomimosaurids (Lee *et al.* 2014; Serrano-Brañas *et al.* 2020) and tyrannosaurids (e.g., Brochu 2003; Holtz 2004) would have been large enough to have pedal unguals that are similar in size



Text-fig. 1. UCM 87636, a right pedal unguis phalanx II-3 of Tyrannosauridae indet., in lateral view (A), medial view (B), dorsal view (C), ventral view (D), and proximal view (E). Abbreviations: ft – flexor tubercle; lcgr – lateral collateral groove; mcgr – medial collateral groove; pas – proximal articular surface. Images are courtesy of The Fossil Vertebrate Collection at the University of Colorado Boulder Museum of Natural History.



Text-fig. 2. 3D model of UCM 87636, a right pedal unguis phalanx II-3 of Tyrannosauridae indet., in lateral view (A), medial view (B), dorsal view (C), ventral view (D), and proximal view (E). Abbreviations: ft – flexor tubercle; lcgr – lateral collateral groove; mcgr – medial collateral groove; pas – proximal articular surface. Images are courtesy of The Fossil Vertebrate Collection at the University of Colorado Boulder Museum of Natural History.

with UCM 87636. UCM 87636 lacks the constricted proximal articular surface and proximally diverging collateral grooves seen in the pedal unguis of large caenagnathids (Xu *et al.* 2007; Lamanna *et al.* 2014). UCM 87636 can be distinguished from ornithomimosaurs by the absence of a distinctive proximal constriction at the base of the unguis as well as the ventral depression with ridge-like flexor tubercle, which are present even in the largest examples of this clade (Longrich 2008; Lee *et al.* 2014; Serrano-Brañas *et al.* 2020). The overall form, as well as details of its anatomy in UCM 87636 match those seen in other tyrannosaurid pedal unguis (see below). Thus, UCM 87636 can be confidently referred to this clade.

COMPARATIVE DESCRIPTION: UCM 87636 resembles the general morphology of large-bodied tyrannosaurid pedal unguis from the Upper Cretaceous deposits of Asia and North America, such as *Alectrosaurus olseni* Gilmore, 1933 (Mader and Bradley 1989, fig. 4), *Appalachiosaurus montgomeriensis* Carr, Williamson and Schwimmer, 2005 (their fig. 20), *Bistahieversor sealeyi* Carr and Williamson, 2010 (Carr and Williamson 2000, fig. 8), *Alioramus remotus* Kurzanov, 1976 (Brusatte *et al.* 2012, fig. 79), *Albertosaurus sarcophagus* (Mallon *et al.* 2020, fig. 16), *Gorgosaurus libratus* (Lambe 1917, figs 6, 7), *Tyrannosaurus rex* (Brochu 2003, figs 105–108), and an unnamed tyrannosaurine from the Aguja

Formation of Texas (Lehman and Wick 2013, fig. 9). Overall, the specimen is nearly complete, except for the distal part of the bone and the lateral part of the proximal articular surface. When measured along the dorsal curve of the preserved bone, UCM 87636 has a length of 55 mm. When the complete ungual is restored using the two-circle method of Fowler *et al.* (2009), the dorsal curve and straight length of the bone are estimated as 119 mm and 82.4 mm, respectively. Such dimensions are close to those of juvenile and subadult tyrannosaurids, but significantly smaller than those of adult *Gorgosaurus libratus* or *Tyrannosaurus rex* (Brochu 2003; Lehman and Wick 2013; Funston *et al.* 2021). UCM 87636 differs from the mediolaterally narrow condition of the pedal ungual of digit I of tyrannosaurids (Brochu 2003; Brusatte *et al.* 2012). Additionally, it curves medially, and its vertical axis is laterally inclined. All of these are consistent with the condition of ungual II-3 in the theropod pes (Lambe 1917; Funston *et al.* 2021). Such features, together with the asymmetry of the collateral grooves, suggest UCM 87636 is the ungual from digit II of the right pes.

The dorsal surface of the bone is strongly convex, and pierced by numerous small foramina (Text-figs 1C, 2C). This may indicate the relative immaturity of the specimen (e.g., Maganuco and Dal Sasso 2018; Funston *et al.* 2021), but it is equally possible that this represents a preservation artifact. The dorsal surface is narrower compared to the ventral surface, which makes the cross-section of the bone triangular.

The proximal articular surface of UCM 87636 is roughly triangular, and its dorsoventral height is 33 mm while the mediolateral width is 25 mm (Text-figs 1E, 2E). Such stout proportions of the pedal ungual are similar to those of subadult and adult tyrannosaurids (Funston *et al.* 2021). There is no sign of a midline vertical ridge in the proximal articular surface of UCM 87636, as in *Bistahieversor sealeyi*, *Gorgosaurus libratus*, *Tarbosaurus bataar* (Maleev, 1955) and *Tyrannosaurus rex*, and UCM 87636 differs from the ungual in *Alectrosaurus olseni*, in which a low vertical ridge is present in all its pedal unguals (Carr 2005). A very slight concavity is present just distal to the proximal articular surface, so UCM 87636 lacks the 'lipped' condition seen in *Appalachiosaurus montgomeriensis*, in which the caudodorsal margins of the pedal unguals are strongly concave and elongated (Carr *et al.* 2005).

In the lateral surface of the ungual, a deep, broad collateral groove incises the body of the bone (Text-figs 1A, 2A). While partially damaged, it appears that the proximal part of the groove is distinctly broader

than the distal part. The distal part of the groove is oriented dorsally.

In the medial surface, a collateral groove is much more weakly developed compared to the lateral groove, such that only a slight, elongated concavity is present in the region (Text-figs 1B, 2B). As in the lateral groove, the proximal part of the medial groove is broader than the distal part, and the distal part is dorsally oriented. Additionally, the medial groove is located ventral to the lateral groove.

The proximal articular surface of UCM 87636 does not invade onto the medial surface of the bone, similar to *Gorgosaurus libratus* (Carr 2005). In *Alectrosaurus olseni*, *Bistahieversor sealeyi* and *Tyrannosaurus rex*, the proximal articular surface extends onto the dorso-medial surface of the bone (Carr 2005).

While the ventral surface of UCM 87636 is gently recurved distally, it is generally flat (Text-figs 1D, 2D). If the missing tip is restored, the internal curvature of the specimen would be about 138°. Such relatively flat, less recurved condition of the pedal ungual is the typical condition in small tyrannosaurid individuals (Mallon *et al.* 2020; Funston *et al.* 2021). The flexor tubercle is low, and is positioned more distally than the proximal articular surface in both lateral and medial views, similar to *Appalachiosaurus montgomeriensis*, *Bistahieversor sealeyi*, *Gorgosaurus libratus* and *Tyrannosaurus rex* (Carr 2005; Mallon *et al.* 2020, fig. 26). This contrasts with *Alectrosaurus olseni* and *Tarbosaurus bataar*, in which the flexor tubercle is hypertrophied and the proximal tip of the tubercle approaches the proximal articular surface of the ungual (Mader and Bradley 1989; Carr 2005). Similar to the dorsal surface, numerous small foramina penetrate the ventral surface of the bone.

DISCUSSION

In terms of absolute size, UCM 87636 is smaller than the unguals from pedal digit II of adult *Gorgosaurus libratus* or *Tyrannosaurus rex*. When the estimated complete length (82.4 mm) is plotted into Funston *et al.* (2021)'s allometric equation comparing the pedal ungual II-3 length (UL) against the body length (BL) in tyrannosaurids ($\text{Log BL} = 0.79242 * \text{Log UL} + 2.2942$; $r^2 = 0.788$, $p \leq 0.001$), the body length of the individual UCM 87636 represents was likely about 6.6 m, which is relatively small for a tyrannosaurid (e.g., Holtz 2004). Given the obvious lack of material, it is currently not possible to determine whether this represents a young individual or a new, small-sized taxon.

As noted by Holtz (2004) and Carr (2005), the postcranial anatomy of later-diverging tyrannosauroids has been generally ignored in the search for systematically informative variation, and most recognized autapomorphies or synapomorphies of taxa within the clade are cranial. Nevertheless, several preliminary attempts have been made to reveal diagnostic characters in the tyrannosauroid postcranial skeleton (e.g., Carr 2005; Carr *et al.* 2005), which allow some meaningful comparisons between UCM 87636 and other tyrannosauroids. Interestingly, UCM 87636 shares one character (proximal articular surface that does not extend onto the dorsomedial surface of pedal ungual II-3) with *Gorgosaurus libratus*, and this feature was considered as one of the autapomorphies of the latter taxon by Carr (2005).

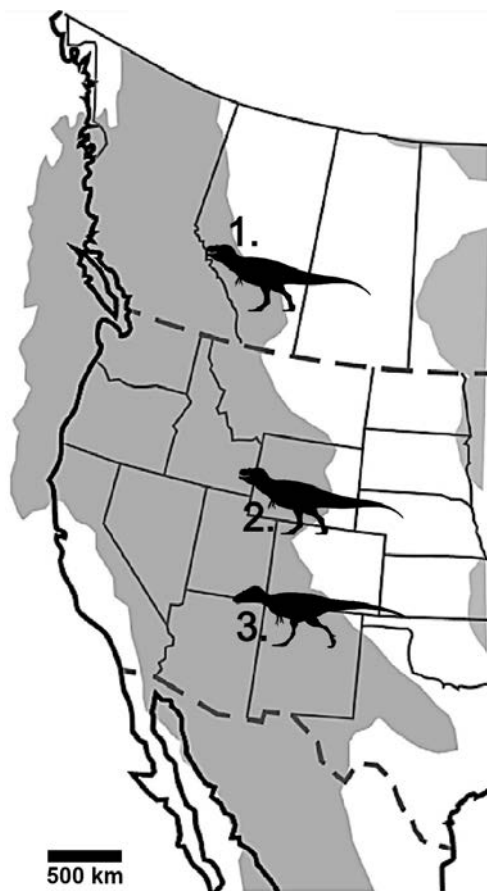
The vertebrate fauna of the Williams Fork Formation is considered as stratigraphically equivalent to (Fowler 2017; Fowler and Freedman Fowler 2020) or slightly younger than (cf. Walker *et al.* 2021) the Hunter Wash Member of the Kirtland Formation, New Mexico. A sister taxon of Tyrannosauridae, *Bistahieversor sealeyi*, occurs in this member (Carr and Williamson 2010), but UCM 87636 is distinguishable from this taxon by the aforementioned morphology of the proximal articular surface (Carr 2005). This may indicate a taxonomic distinction between UCM 87636 and *Bistahieversor sealeyi*. However, at present it is premature to assign UCM 87636 to *Gorgosaurus libratus*, as interspecific/intraspecific variation in tyrannosauroid postcrania is still poorly understood (e.g., Holtz 2004) and only one shared character based on limited material is currently identified. If pedal ungual fossils of other tyrannosaurid taxa (e.g., *Teratophoneus curriei* Carr, Williamson, Britt and Stadtmann, 2011) from other strata of similar age (e.g., Kaiparowits Formation; Foster and Hunt-Foster 2015) are also found and described, a detailed comparison with them seems necessary.

Together with UCM 87636, Diem (1999) briefly described some isolated tyrannosaurid teeth from the Williams Fork Formation. While Brand *et al.* (2022) included aff. *Albertosaurus* and aff. *Daspletosaurus* in their vertebrate faunal list of the Williams Fork Formation, no information was given on which specimens these identifications are based on. Given that instances of sympatry among Late Cretaceous Laramidian tyrannosauroids are rare (Carr *et al.* 2011, 2017), it is possible that all of these materials belong to the same taxon. Among these, UCM 57543 is a premaxillary tooth that was likely shed from a small juvenile, given its small size (crown height slightly more than 20 mm; Diem 1999, fig. 21). Intriguingly, both

carinae are serrated in this specimen (Diem 1999), which is reminiscent of the condition in albertosaurines, in which serrations are already present in premaxillary teeth of the smallest juveniles (Currie 2003; Funston *et al.* 2021). In contrast, juvenile tyrannosaurines often lack serrations in premaxillary tooth carinae (Currie 2003; Funston *et al.* 2021). Additionally, albertosaurine premaxillary teeth might be distinguishable from those of large tyrannosaurines (e.g., *Tarbosaurus bataar*, *Tyrannosaurus rex*) by their relatively blunt, chisel-like apices, whereas apices of tyrannosaurine premaxillary teeth are pointed, and spike-like (N. Longrich, pers. comm., June 2022). A blunt, chisel-like apex is present in UCM 57543 (Diem 1999, fig. 21). However, at least one tyrannosaurine taxon (*Tarbosaurus bataar*) is known to possess serrated premaxillary teeth at a relatively young growth stage (Tsuihiji *et al.* 2011), and cases of relatively blunt apices of juvenile tyrannosaurine premaxillary teeth are known (e.g., Molnar 1978, fig. 5; Gates *et al.* 2015, fig. 2G). In summary, none of the currently recognized tyrannosaurid material from the Williams Fork Formation appears to support the definite occurrence of an albertosaurine in the fauna.

Nevertheless, if a hypothesis that UCM 87636 represents a tyrannosaurid taxon that is closely related to northern Laramidian taxa such as *Gorgosaurus libratus* is correct, it bears some important implications. Firstly, its potential distinctiveness from the geographically and temporally close taxon *Bistahieversor sealeyi* may support the idea that Laramidian dinosaurs were highly endemic during the Campanian (e.g., Lehman 1987; Sampson *et al.* 2010; Longrich 2014; Bell *et al.* 2015; Dalman *et al.* 2022), including tyrannosaurids (e.g., Carr *et al.* 2011; Voris *et al.* 2020). Secondly, its morphological similarity with *Gorgosaurus libratus* opens the possibility that tyrannosaurid lineages (e.g., Albertosaurinae Currie, Hurum and Sabath, 2003; Daspletosaurini Voris, Therrien, Zelenitsky and Brown, 2020) that were thought to be endemic to northern Laramidia (Carr *et al.* 2017; Voris *et al.* 2020) may have had a broader distribution (Text-fig. 3). Indeed, multiple Campanian dinosaur lineages occurring in both northern and southern parts of Laramidia have been reported (e.g., Longrich 2014), and a parsimony analysis of Brusatte and Carr (2016) suggests at least one tyrannosaurid lineage (*Teratophoneus–Nanuqsaurus*) may have had a broad distribution throughout Laramidia.

Of note, Longrich (2014) provisionally referred a ceratopsid skull (SDNHM 43470) from the Williams Fork Formation (Diem and Archibald 2005) to *Pentaceratops aquilonius* Longrich, 2014, mainly



Text-fig. 3. A hypothetical tyrannosauroid diversity and distribution in western North America (Laramidia) during the late Campanian. 1 – *Gorgosaurus libratus* from the Dinosaur Park Formation of Alberta, an exemplary northern Laramidian tyrannosauroid taxon; 2 – A tyrannosauroid taxon from the Williams Fork Formation of Colorado with pedal ungual anatomy that is similar to *Gorgosaurus libratus*; 3 – *Bistahieversor sealeyi* from the Kirtland Formation of New Mexico, an exemplary southern Laramidian tyrannosauroid. Map modified from Bell *et al.* (2015), taxon silhouettes from phylopic.org (*Bistahieversor*: Christopher Chávez; *Gorgosaurus*: Tasman Dixon).

based on a similar phylogenetic position. Of note, the taxonomic identity of SDNHM 43470 has been controversial. Some scholars have regarded this specimen as indeterminate Chasmosaurinae (Diem and Archibald 2005), but the general view is that it belongs to or is closely related to at least the genus *Pentaceratops* (Lucas *et al.* 2006; Fowler and Freedman Fowler 2020; Dalman *et al.* 2022). All the definitive material of *Pentaceratops aquilonius* are from the Dinosaur Park Formation (Longrich 2014), and this taxon is considered to be a form similar to the Judith River Formation taxon *Spiclypeus shipporum* Mallon, Ott, Larson, Juliano and Evans, 2016, or a northern representative of the *Utahceratops*–

Pentaceratops lineage (Fowler and Freedman Fowler 2020; Dalman *et al.* 2022). Fossils of *Gorgosaurus libratus* occur in both the Dinosaur Park and Judith River formations (Voris *et al.* 2022). Thus, the cases of SDNHM 43470 and UCM 87636 suggest the dinosaur fauna of the Williams Fork Formation may have resembled those of the Dinosaur Park Formation or Judith River Formation.

Lastly, based on crocodyliform fossils, Foster and Hunt-Foster (2015) proposed that the Williams Fork Formation paleoenvironment may have been within the biogeographic transition zone between the northern and southern faunas of Campanian Laramidia. Of note, Thomson *et al.* (2013) suggested such a boundary between the northern and southern assemblages may have been at the same latitude with the Williams Fork Formation fauna, based on tyrannosauroid metatarsals from the Nelsen Formation of Utah that were proposed to be similar to those of northern taxa (i.e., Albertosaurinae, *Daspletosaurus* spp.). Various mechanisms, such as flora, climate, geographical barriers, and competition with dinosaurs of closely related species, have been identified as factors leading to the provincialism of these Laramidia dinosaurs (e.g., Longrich 2014), but it is still unclear what was the main factor (Lucas *et al.* 2016). Perhaps it is a combined result of all of these mechanisms, and at least some of the faunas which have been compared to support this hypothesis are slightly different in age, so the difference in the faunas of individual members may actually be due to the difference in age (Lucas *et al.* 2016; Dalman *et al.* 2022). The proposed character evidence (presence or absence of the ridge in the caudal surface of metatarsal IV) was included in the phylogenetic analysis of Loewen *et al.* (2013), but the utility of this feature was questioned by Brusatte and Carr (2016). The resemblance of UCM 87636 with pedal ungual II-3 of *Gorgosaurus libratus*, lends some support to the hypotheses of Thomson *et al.* (2013) and Foster and Hunt-Foster (2015).

Interestingly, UCM 87636 differs from the pedal unguals of *Alectrosaurus olseni* and *Tarbosaurus bataar* but is consistent with the typical tyrannosauroid condition by lacking a hypertrophied flexor tubercle that approaches the proximal articular surface (Mader and Bradley 1989; Carr 2005). Carr (2005) found that such a flexor tubercle in *Alectrosaurus olseni* is reminiscent to those of raptorial and large cursorial birds, and hypothesized that this feature is indicating an enhanced cursorial ability of this taxon. However, an enlargement of the flexor tubercles on pedal unguals may also be related to an increase of the



Text-fig. 4. A reconstruction of the tyrannosaurid taxon from the Williams Fork Formation, preying on a contemporaneous ceratopsid taxon that is represented by SDNHM 43470. Artwork by Jun-Hyeok Jang.

grip strength of the pes (Fowler *et al.* 2011), and this potentially suggests *Alectrosaurus olseni* suppressed its prey with its jaws as well as its relatively strong, gripping hind paws. If this hypothesis is correct, the tyrannosaurid of the Williams Fork Formation, unlike *Alectrosaurus olseni*, may not have used its hind paws for hunting and, like most other tyrannosaurids (e.g., Holtz 2004, 2008), may have used mainly strong jaws for hunting (Text-fig. 4).

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