

PROBABLE JUVENILE FRONTAL OF *DASPLETOSAURUS HORNERI* (DINOSAURIA: THEROPODA) FROM THE TWO MEDICINE FORMATION OF MONTANA, WITH IMPLICATIONS FOR TYRANNOSAURID ONTOGENY

Chan-gyu Yun

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Abstract A partial left frontal (UCM 55499) of a small tyrannosaurid theropod from the Campanian Two Medicine Formation of Montana is described, and is considered to probably represent a juvenile of *Daspletosaurus horneri*. UCM 55499 compares favorably with the frontals of other young juvenile tyrannosaurid specimens, and its diminutive size suggests that the element comes from a small juvenile individual. Differences (including width of the nasal process, and degree of expansion of the postorbital buttress and the caudal shelf) between it and frontals of the larger individuals of *Daspletosaurus horneri* are similar to those between juveniles and adults of other tyrannosaurids such as *Tyrannosaurus rex*, suggesting that overall ontogenetic trends in the frontal bone of *Daspletosaurus horneri* are largely consistent with the patterns seen in other tyrannosaurids.

Keywords: Juvenile, Frontal, Theropoda, Tyrannosauridae, *Daspletosaurus*, *Tyrannosaurus*

INTRODUCTION

Ontogenetic changes in the cranial anatomy of tyrannosaurid theropods have been described in substantial detail for several taxa, based on the study of well-preserved skulls or isolated cranial elements (e.g., Carr, 1999, 2020; Currie, 2003a, b; Carr & Williamson, 2004). These descriptions have demonstrated that patterns of cranial change during the ontogeny of tyrannosaurids are largely shared between different species (Carr, 1999), and have made it possible to establish the correct taxonomic identities of some initially misclassified juvenile or subadult specimens (e.g., Carr, 1999; Currie, 2003b; Carr & Williamson, 2004; Tsuihiji et al., 2011; Fowler et al., 2011; Voris et al., 2019, 2022). Despite these thorough descriptions of tyrannosaurid cranial ontogeny, the degree to which ontogenetic patterns are shared across species is still a matter of debate, as treatments of tyrannosaurid ontogeny have largely been focused on taxa known from individuals ranging from small juveniles to large adults, such as *Gorgosaurus libratus* or *Tyrannosaurus rex* (Carr, 1999, 2020). Other taxa have received relatively scant attention, mostly due to a lack of specimens representing multiple growth stages (e.g., Voris et al., 2019). *Daspletosaurus horneri* is a species that currently represents the geologically youngest member of the lineage Daspletosaurini, and is from the Two Medicine Formation of Montana, USA (Carr et al., 2017; Voris et al., 2020). Specimens that represent different ontogenetic stages of this taxon are known (Carr et al., 2017). Unfortunately, while well-preserved skulls of a large subadult and an adult are known, reported young juvenile and small subadult specimens of this taxon are limited to isolated elements such as a dentary or a maxilla (Carr et al., 2017; Delcourt, 2017), so that inferences about ontogenetic change are limited to these parts of the skeleton.

Currie et al. (2005) reported a tyrannosaurid bonebed with individuals of different sizes which are probably referable to *Daspletosaurus horneri*, but the recovered material was only briefly described. An embryonic dentary (MOR 268) was recently assigned provisionally to this taxon (Funston et al., 2021) but it is equally possible that this specimen belongs to the contemporaneous species *Gorgosaurus libratus* (Yun, 2021). In sum, current data about the ontogeny of *Daspletosaurus horneri* is limited.

In this work, a partial left frontal (UCM 55499) of a juvenile tyrannosaurid from the Two Medicine Formation, which is probably referable to *Daspletosaurus horneri*, is described in detail. This specimen provides an opportunity to infer ontogenetic changes in the frontal bone of *Daspletosaurus horneri* and to compare the juvenile morphology of the frontal of this taxon with those of other young tyrannosaurids.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; CMNH, Cleveland Museum of Natural History, Ohio, USA; LACM, Los Angeles County Museum of Natural History, California, USA; MOR, Museum of the Rockies, Montana, USA; MPC-D, Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; TMP, Royal Tyrrell Museum of Palaeontology, Alberta, Canada; UCM, The Fossil Vertebrate Collection at the University of Colorado Boulder Museum of Natural History, Colorado, USA.

MATERIAL AND METHODS

Because of travel restrictions that were imposed in response to the COVID-19 pandemic, this study was mainly conducted using a high-quality cast, as well as a scan, of the original specimen shared by the UCM collections manager Jacob Van Veldhuizen. Comparisons with other tyrannosaurid specimens and other theropod clades were made through prior observation of several specimens and a review of the literature. Angles between the postorbital suture/frontal suture and the rostrocaudal axis of frontal/postorbital were measured from images using the program ImageJ (Schneider et al., 2012). *Alioramus altai* is considered a junior synonym of *Alioramus remotus* following Carr et al. (2017). Following Currie (2003a) and Paulina-Carabajal et al. (2021), specimens of *Daspletosaurus* from the Dinosaur Park Formation are referred to *Daspletosaurus* sp. to reflect the possibility that they represent a distinct taxon from the type species of the genus, *Daspletosaurus torosus* (contra Carr et al., 2017). Anatomical terminology for the frontal follows Currie (2003a), Carr et al. (2017), Yun (2020), and Yun (2022).

GEOLOGICAL SETTING

UCM 55499 was recovered from the Two Medicine Formation of Montana, USA. Unfortunately, more detailed provenance data for the specimen is missing. However, it is likely that this specimen was collected from the upper section of this formation, as reported tyrannosaurid fossils from the Two Medicine Formation have mainly been restricted to this part (e.g., Currie et al., 2005; Carr et al., 2017; Dalman et al., 2018; Funston et al., 2021; Yun, 2021). This is further supported by the high probability that UCM 55499 belongs to *Daspletosaurus horneri*, as all known material definitely attributable to this taxon comes from the upper section of the Two Medicine Formation (Currie et al., 2005; Carr et al., 2017).

The thickness of the Two Medicine Formation is 600 m to 1500 m (Fowler, 2017). The formation is composed of fine-grained lenticular sandstone, mudstone and siltstone, and these sediments were derived from erosion of the rising Sevier Thrust Belt and the Elkhorn Mountains Volcanics (e.g., Rogers et al., 1993; Penkalski, 2014; Panasci & Varricchio, 2020). Deposition of the formation occurred in a volcanically active area with a paleolatitude of about 53–55° N, in which fluvial and lacustrine systems intergraded (e.g., Freimuth & Varricchio, 2019; Freimuth et al., 2021). ⁴⁰Ar/³⁹Ar radiometric dates near the base and the top of the Two Medicine Formation constrain the age of the formation to between 81.5 Ma and 75 Ma (Rogers et al., 1993; Fowler, 2017). Therefore, the age of the Two Medicine Formation is middle to late Campanian. The Two Medicine Formation is well-known for its rich abundance of vertebrate fossils, and especially of dinosaur specimens that include well-preserved skeletons, as well as coprolites, eggs, gastric pellets and nests (e.g.,

Rogers, 1997; Trexler, 2001; Freimuth et al., 2021). Patterns of preservation of dinosaur fossils vary within the formation: the fossils from the lower half are generally rare, and are mostly isolated bones and teeth (Rogers, 1997; Trexler, 2001) whereas the upper part of the formation is remarkably fossiliferous, containing most of the dinosaur bonebeds and nests reported from the formation (Rogers, 1997). Dinosaurian clades documented within the Two Medicine Formation include ankylosaurs, avialans, ceratopsians, dromaeosaurids, ornithomimosaurs, ornithomimosaurids, troodontids, and tyrannosaurids (e.g., Trexler, 2001; Varricchio, 2001; Dalman et al., 2018; Freimuth et al., 2021).

SYSTEMATIC PALAEOLOGY

Tyrannosauroidae Osborn, 1906

Tyrannosauridae Osborn, 1906

Tyrannosaurinae Osborn, 1906

Daspletosaurini Voris et al., 2020

cf. *Daspletosaurus* Russell, 1970

cf. *Daspletosaurus horneri* Carr et al., 2017

Material: UCM 55499, a left juvenile frontal of a tyrannosaurid theropod (Figs. 1, 2).

Horizon and age: Upper Cretaceous (Campanian) Two Medicine Formation, Montana, USA.

Taxonomic referral: UCM 55499 is referable to Tyrannosauridae and not to any other contemporaneous theropod clade (e.g., Dromaeosauridae, Ornithomimosauria, Troodontidae) based on several features that are unique to tyrannosaurids, including rostrocaudally short orbital slot, expanded postorbital suture which occupies caudal half of the bone and is divided into a postorbital buttress and a caudal shelf, extensive dorsotemporal fossa that covers the entire dorsal surface of the bone caudal to the orbital slot and would have met the opposing fossa at the midline, flat “forehead” (sensu Carr & Williamson, 2010) region, sagittal crest that extends onto the frontal, and frontoparietal suture that projects rostrally along the midline (e.g., Currie, 1987; Tsuihiji et al., 2012; Lehman & Wick, 2013; Carr et al., 2017; Figs. 1, 2). Currently, two tyrannosaurid taxa are recognized in the Two Medicine Formation fauna, namely the albertosaurine *Gorgosaurus libratus* and the tyrannosaurine *Daspletosaurus horneri* (Carr et al., 2017; Dalman et al., 2018; Yun, 2021). In lateral view, the postorbital suture in UCM 55499 slopes caudoventrally, which is similar to tyrannosaurines but differs from the horizontal condition in albertosaurines (Voris, 2018). Indeed, a juvenile postorbital of *Daspletosaurus* (TMP 2013.018.0011) from the Dinosaur Park Formation reported by Voris et al. (2019) preserves a frontal suture that slopes more caudoventrally compared to similarly-sized *Gorgosaurus* frontals (Voris, 2018; J.T. Voris pers. comm.). The angle between the frontal suture and the rostrocaudal axis of the bone in the medial

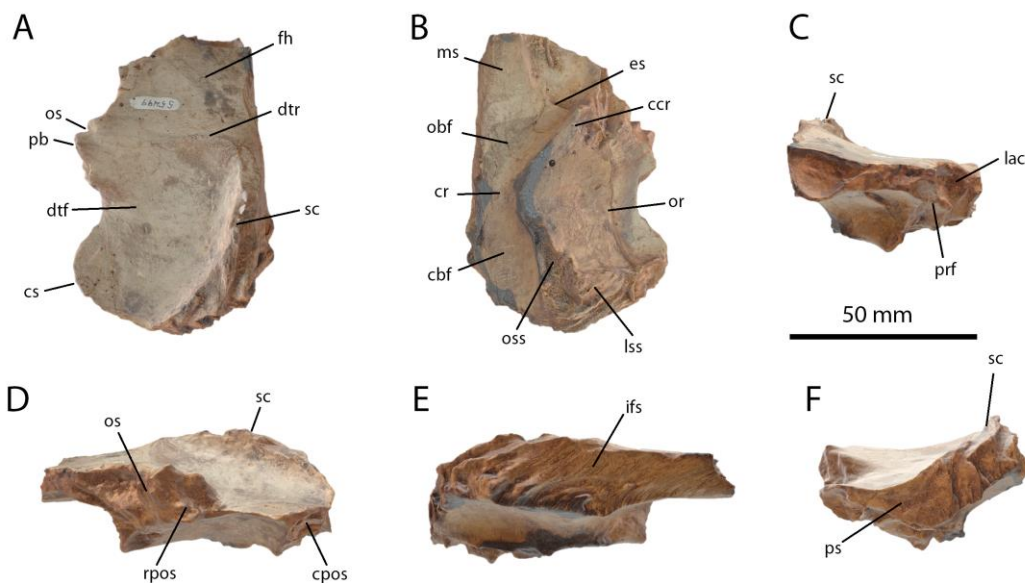


Fig. 1 UCM 55499, left frontal of a juvenile cf. *Daspletosaurus horneri*, in A, dorsal view; B, ventral view; C, rostral view; D, lateral view; E, medial view; F, caudal view. **Abbreviations:** **cbf**, cerebral fossa; **ccr**, crista cranii; **cpos**, caudal part of postorbital suture; **cr**, cylinder-like ridge; **cs**, caudal shelf; **dtf**, dorsotemporal fossa; **dtr**, dorsotemporal ridge; **es**, ethmoid scar; **fh**, forehead region; **ifs**, interfrontal suture; **lac**, lacrimal socket; **lss**, laterosphenoid suture; **ms**, joint surface for the mesethmoid; **obf**, olfactory bulb fossa; **or**, orbital wall; **os**, orbital slot; **oss**, orbitosphenoid suture; **pb**, postorbital buttress; **prf**, joint surface for prefrontal; **ps**, parietal suture; **rpos**, rostral part of postorbital suture; **sc**, sagittal crest. Images are courtesy of The Fossil Vertebrate Collection at the University of Colorado Boulder Museum of Natural History.

surface of TMP 2013.018.0011 (14.2°; Voris et al., 2019: fig. 2) and that of the postorbital suture and the rostrocaudal axis (19.7°) in the lateral surface of UCM 55499 are comparable to each other. Additionally, the laterosphenoid suture in UCM 55499 is facing caudoventrally, unlike the subvertical, caudally-facing suture in *Gorgosaurus* frontals (e.g., Yun, 2020; pers. obs). This appears to be consistent with the description of Voris (2018), who noted the angle between frontal and laterosphenoid sutures in *Daspletosaurus* postorbitals is obtuse, in which the former slopes caudoventrally. Furthermore, the mediolateral width of the caudal shelf in UCM 55499 is slightly wider than that of the postorbital buttress, which is reminiscent to the condition in tyrannosaurines (Voris, 2018; Voris et al., 2022). In contrast, the widest part of the albertosaurine frontals is located at the rostral end of postorbital suture (Voris, 2018; Voris et al., 2022). Thus, UCM 55499 can be identified as a tyrannosaurine, of which *Daspletosaurus horneri* is the only known example in the Two Medicine Formation. Therefore, this specimen is probably referable to this taxon. Of note, UCM 55499 does resemble *Gorgosaurus* frontals by possessing mediolaterally oriented orbital slot in dorsal view (Voris et al., 2022) but it is interpreted in this work that this apparent similarity is likely due to the “transitional” growth stage that the specimen represents, between small juveniles with rostrocaudally elongated shallow slot (Carr, 1999; Tsuihiji et al., 2011) and the folded, narrow and deep slot present in tyrannosaurine adults (Carr, 2020; Voris et al., 2022), or else as an indi-

vidual variation. Furthermore, the area between the postorbital buttress and the caudal shelf in UCM 55499 is extremely thin and plate-like, similar to the condition reported in the holotype of tyrannosaurine *Alioramus “altai”* (Bever et al., 2013) but differs from the relatively deep condition in juvenile *Gorgosaurus* (e.g., Voris et al., 2019: fig. S15). Lastly, *Gorgosaurus* does not approach the abundance of *Daspletosaurus horneri* in the Two Medicine Formation (e.g., Farlow & Pianka, 2002; Carr et al., 2017; Voris et al., 2020). In summary, the combination of aforementioned *Daspletosaurus*-like or tyrannosaurine-like features, differences from similarly-sized *Gorgosaurus* frontals as well as its provenance favours identification of the specimen as *Daspletosaurus horneri* through a balance of probability.

Comparative description: UCM 55499 is an isolated, mostly complete left frontal that lacks the nasal process, the rostral part of the area that articulated with the prefrontal, and the dorsal part of the sagittal crest. As preserved, the maximum rostrocaudal length of the specimen is 82 mm. When measured after the methodology of Currie (2003a), the width and depth are 44 mm and 18 mm, respectively. The specimen is comparable in its dimensions to small frontals of *Daspletosaurus* sp., *Gorgosaurus libratus*, *Tarbosaurus bataar*, and *Tyrannosaurus rex*, but much smaller than large frontals of any of these (Currie, 2003a; Lehman & Wick, 2013). The subcutaneous surface of the “forehead” region is flat, like in some individuals of *Daspletosaurus* spp., and in *Lythronax argestes* (Voris et al., 2020; Yun, 2020; Figs.

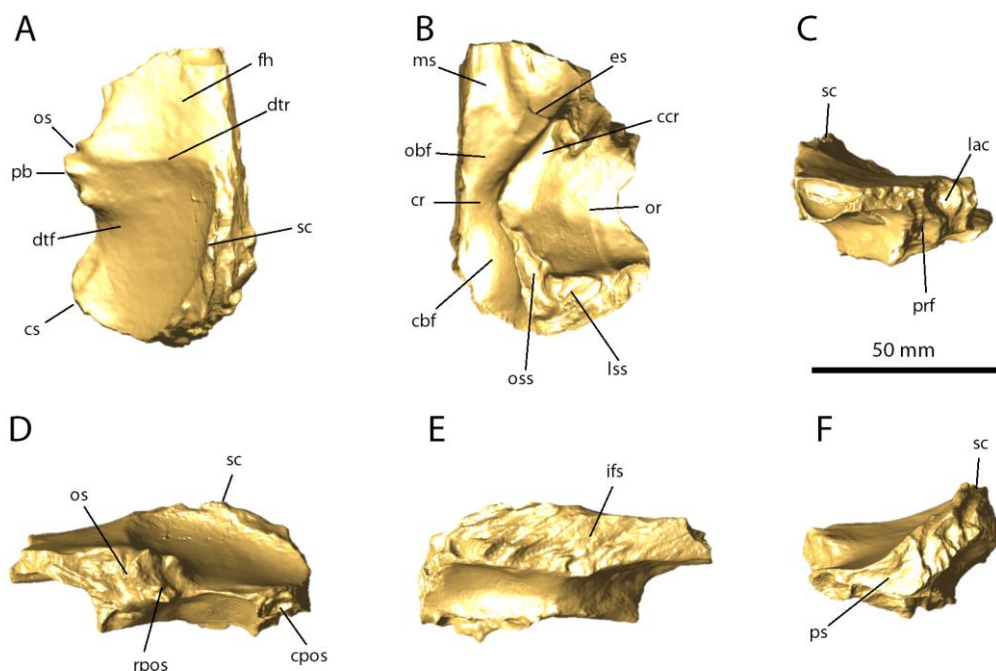


Fig. 2 3D model of UCM 55499, left frontal of a juvenile cf. *Daspletosaurus horneri*, in A, dorsal view; B, ventral view; C, rostral view; D, lateral view; E, medial view; F, caudal view. **Abbreviations:** **cbf**, cerebral fossa; **ccr**, crista cranii; **cpos**, caudal part of postorbital suture; **cr**, cylinder-like ridge; **cs**, caudal shelf; **dtf**, dorsotemporal fossa; **dtr**, dorsotemporal ridge; **es**, ethmoid scar; **fh**, forehead region; **ifs**, interfrontal suture; **lac**, lacrimal socket; **lss**, laterosphenoid suture; **ms**, joint surface for the mesethmoid; **obf**, olfactory bulb fossa; **or**, orbital wall; **os**, orbital slot; **oss**, orbitosphenoid suture; **pb**, postorbital buttress; **prf**, joint surface for prefrontal; **ps**, parietal suture; **rpos**, rostral part of postorbital suture; **sc**, sagittal crest. The model is courtesy of The Fossil Vertebrate Collection at the University of Colorado Boulder Museum of Natural History.

1A, 2A). Caudally, a large but shallow dorsotemporal fossa is present, and would have occupied at least half of the entire subcutaneous surface when the bone was complete, like in other derived tyrannosaurines (Carr et al., 2017; Figs. 1A, 2A). While the nasal process is broken in UCM 55499, the frontal is wide at the rostromedial level of the joint surface for the prefrontal, indicating the base of the nasal process was transversely wide as well (Figs. 1A, B, 2A, B). This is similar to the condition in albertosaurines and juvenile tyrannosaurines, which have a wide nasal process (Carr, 1999; Carr & Williamson, 2004, 2010; Lehman & Wick, 2013) but differs from the transversely narrow process in subadults and adults of the latter clade (Carr & Williamson, 2004, 2010; Lehman & Wick, 2013; Yun, 2020, 2022). The apex of the joint surface for the prefrontal is narrow in UCM 55499, indicating that the prefrontal was narrowly exposed on the skull roof of this individual (Figs. 1C, 2C). This contrasts with the broad, teardrop-shaped prefrontal of adult daspletosaurines (Voris et al., 2020). Ventrally, the trace of the prefrontal contact suggests that the prefrontal had only one medially projecting prong, like all other tyrannosaurids excepting *Thanatotheristes* which has two ventral prongs on the prefrontal (Voris et al., 2020; Yun, 2020, 2022).

Laterally, there is a rostrally facing, cup-shaped lacrimal contact that is similar to those in *Daspletosaurus* spp., *Gorgosaurus libratus*, *Nanuqsaurus hoglundi*,

Teratophoneus curriei, and several examples of *Tyrannosaurus rex* (Currie, 2003a; Fiorillo & Tykoski, 2014; Yun, 2020, 2022). Dorsally, the medial and caudal margins of the socket are continuous, forming a crescent shape (Figs. 1A, 2A) that differs from the right-angled shape observed in some tyrannosaurid frontals (Currie, 2003a; Yun, 2020, 2022). Nevertheless, the medial margin is elongated while the caudal margin is narrow, as in juvenile tyrannosaurids (Carr, 1999; Carr & Williamson, 2004). Caudolateral to the lacrimal socket is a narrow, groove-like, deep orbital slot that is oriented subvertically (Figs. 1D, 2D). This differs from the rostrocaudally broad shallow condition seen in small juveniles of *Tarbosaurus bataar* and *Tyrannosaurus rex* (Carr, 1999; Carr & Williamson, 2004; Tsuihiji et al., 2011). The apex of this slot is slightly inclined rostrally. Medial to the orbital slot there is a weakly developed, sinuous, mediolaterally oriented dorsotemporal ridge (Figs. 1A, 2A). This differs from the rostrolaterally oriented condition seen in large individuals of *Daspletosaurus horneri* but agrees with the condition seen in most tyrannosaurines (Carr et al., 2017; Voris et al., 2020).

Caudal to the orbital slot on the lateral surface of the frontal, a postorbital buttress bears the rostral part of the postorbital suture. The rostral part of the postorbital suture is circular, and considerably shallower (13 mm in dorsoventral depth) than in large subadult and adult tyrannosaurines (Carr & Williamson, 2004; Voris et al.,

2020; Yun, 2020). Nevertheless, both the degree of dorsoventral expansion as well as its overall morphology closely matches those of the rostral part of the frontal sutural surface of a juvenile *Daspletosaurus* postorbital (Voris et al., 2019). Additionally, it is slightly concave and marked by distinct ridges and grooves (Figs. 1D, 2D), as in juveniles of *Alioramus remotus* and *Tyrannosaurus rex* (Carr & Williamson, 2004; Bever et al., 2013). The caudal part of the postorbital suture is even shallower than the rostral part (11 mm in depth), and is oriented caudoventrally. The caudal shelf that marks the caudal part of the postorbital suture is transversely extended, and its mediolateral width (53 mm) is slightly greater than that of the postorbital buttress (50 mm). The rostral and caudal parts of the postorbital suture in UCM 55499 are separated by an interval of thin margin (less than 1 mm in depth) laterally, similar to the condition seen in juvenile *Alioramus remotus* (Bever et al., 2013). In larger tyrannosaurine individuals the two parts of the postorbital suture are more closely spaced and dorsoventrally deep (e.g., Currie, 2003a; Hurum & Sabath, 2003; McDonald et al., 2018; Yun, 2020, 2022). In lateral view, the entire postorbital suture slopes caudoventrally at an angle of approximately 19.7° , similar to other tyrannosaurines including juvenile individuals (e.g., Tsuihiji et al., 2011: fig. 10; Fiorillo & Tykoski, 2014: fig. 3; Bever et al., 2013: fig. 3; Voris, 2018; Voris et al., 2019: fig. 2; Paulina-Carabajal et al., 2021: figs. 2, 3) but unlike the horizontally oriented condition in albertosaurines (e.g., Currie, 2003a: figs. 7, 8, 22; Voris, 2018; Voris et al., 2022; pers. Obs.). Caudally, the frontoparietal suture is oriented slightly rostromedially. Therefore, the overall outline of the frontoparietal suture in UCM 55499 is resembling the wedge-shaped condition seen in larger specimens of *Daspletosaurus horneri* (Carr et al., 2017).

The sagittal crest of UCM 55499 is rostrocaudally elongate (52 mm), forming the entire medial part of the dorsoventral fossa (Figs. 1D, 2D). Such an elongate, well-developed sagittal crest is a typical feature in derived tyrannosaurines that are phylogenetically nested between Alioramini and the *Tarbosaurus bataar* + *Tyrannosaurus rex* clade (e.g., Carr, 1999; Carr & Williamson, 2004; Lehman & Wick, 2013; Carr et al., 2017; McDonald et al., 2018; Voris et al., 2020; Yun, 2020, 2022). The sagittal crest is rostrally extended to a similar degree in CMNH 7541, a juvenile *Tyrannosaurus rex* specimen in which the frontal has similar dimensions to UCM 55499 (Carr, 1999; Currie, 2003a). While the dorsal part of the sagittal crest is broken in UCM 55499, the curvature of the bone grain that is lateral to the crest strongly indicates that the sagittal crest would have been dorsoventrally tall as well (Figs. 1F, 2F), like in derived tyrannosaurines (e.g., Currie, 2003a; Lehman & Wick, 2013; Carr et al., 2017; McDonald et al., 2018; Voris et al., 2020; Yun, 2020, 2022). The orientation of the caudal part of the sagittal crest suggests the rostral extent of the median spur of the parietal that separated the frontals caudally was slight.

The interfrontal surface occupies the entire medial surface of the bone, and is vertical (Figs. 1E, 2E). While the rostral part of the suture is generally flat, a series of distinct ridges appears caudally. The ridges suggest that the frontals interdigitated with each other in this area, like in larger tyrannosaurid individuals (e.g., Currie, 2003a; Yun, 2020, 2022). In a *Tarbosaurus bataar* juvenile considered to be two to three years old (MPC-D 107/07), this area is smooth (Tsuihiji et al., 2011).

A distinct, transversely wide (10 mm) joint surface for the mesethmoid is situated at the rostromedial corner of the ventral surface of the frontal, as in *Gorgosaurus libratus* and *Daspletosaurus* spp. (Yun, 2020; Paulina-Carabajal et al., 2021: fig. 2). This feature differs from the narrow joint surface seen in *Alioramus remotus* and *Teratophoneus curriei* (Bever et al., 2013; Yun, 2022). Lateral to the joint surface for the mesethmoid there is a concave region that represents the caudal end of the nasal cavity, which would have been lined with olfactory epithelium when the animal was alive (e.g., Bever et al., 2013; McDonald et al., 2018; Yun, 2022). Caudally, a short, distinct and ridge-like ethmoid scar separates the nasal cavity from the olfactory bulb fossa (Figs. 1B, 2B). The olfactory bulb fossa is rectangular, and is bounded by the joint surface for the mesethmoid and ethmoid scar rostrally, and the crista cranii laterally (Figs. 1B, 2B). The width and length of this fossa are 24 mm and 25 mm, respectively. The crista cranii is a thick, process-like structure whose rostral portion trends rostromedially as in other tyrannosaurids (Ali et al., 2008; Bever et al., 2013; Yun, 2022). Caudally, a deep, wide (20 mm) and ovoid cerebral fossa is separated from the olfactory bulb fossa by a thick, cylinder-like ridge, similar to other tyrannosaurids (Carr, 2020; Yun, 2022; Figs. 1B, 2B). The rostrocaudal length of the endocranial region in UCM 55499 is therefore 64 mm. Lateral to the cerebral fossa lies the orbitosphenoid suture, which is an ovoid concavity that faces medioventrally (Figs. 1B, 2B), as in other tyrannosaurids (McDonald et al., 2018; Yun, 2020, 2022). The caudoventrally facing laterosphenoid suture is square-shaped, and located caudolateral to the orbitosphenoid suture. The orbital wall occupies a large part of the lateral portion of the ventral surface, and is a half-moon shaped concavity that is bounded by the crista cranii and the orbitosphenoid suture laterally, and by the laterosphenoid suture caudally.

DISCUSSION

Ontogenetic status of UCM 55499: Specimen UCM 55499 can be confidently interpreted as coming from a juvenile individual based on several features that are shared with specimens considered to be juveniles of other tyrannosaurids, such as *Gorgosaurus libratus*, *Tarbosaurus bataar*, and *Tyrannosaurus rex* (Carr, 1999, 2020; Carr & Williamson, 2004; Tsuihiji et al., 2011). The specimen is diminutive in size, the mediolateral width of the bone at the level of the orbital slot being most similar

to the corresponding measurement in tyrannosaurid specimens (e.g., CMNH 7541) which are considered young juveniles (Carr, 1999; Currie, 2003a). It has been demonstrated that body size correlates with maturity for tyrannosaurids at juvenile-subadult growth stages (e.g., Carr, 2020), and that young tyrannosaurids of different species had similar body sizes at equivalent ages (e.g., Erickson et al., 2004; Funston et al., 2021).

Additionally, several morphological features other than small size also indicate the immature status of UCM 55499. The lacrimal socket is longer than wide (Figs. 1A, 2A), and such an elongated but narrow socket is consistent with the condition seen in juveniles of *Gorgosaurus libratus*, *Tarbosaurus bataar*, and *Tyrannosaurus rex* (Carr, 1999, 2020; Carr & Williamson, 2004; Tsuihiji et al., 2011). The dorsotemporal ridge is only weakly developed, similar to juveniles of *Tarbosaurus bataar* and *Tyrannosaurus rex* (Carr & Williamson, 2004; Tsuihiji et al., 2011), but differing from larger subadult and adult tyrannosaurids, in which this ridge is distinctly developed (Currie, 2003a; Carr & Williamson, 2004; Carr et al., 2017). The dorsotemporal fossa is shallow (Figs. 1A, 2A), unlike the deep condition seen in larger and more mature individuals, but similar to the condition previously reported from juvenile tyrannosaurids (Carr, 1999; Carr & Williamson, 2004). Although the rostral and caudal parts of the postorbital suture are well separated and each developed into a postorbital buttress and caudal shelf (Figs. 1A, 2A), they are not as transversely expanded as in large subadults and adults (Carr, 1999, 2020; Carr & Williamson, 2004). The mediolateral width of the tyrannosaurid frontal is strongly positively allometric with respect to skull length (Currie, 2003b), and the underdeveloped buttress and shelf in UCM 55499 closely match the condition found in juvenile *Gorgosaurus libratus* and *Tyrannosaurus rex* (Carr, 1999, 2020). Lastly, UCM 55499 is dorsoventrally shallow, being only 18 mm deep at the medial surface directly rostral to the dorsotemporal fossa. Frontal depth is strongly positively allometric with respect to frontal width in tyrannosaurids (Currie, 2003a), so the dorsoventrally shallow condition of UCM 55499 is consistent with its juvenile status. It is also noteworthy that the postorbital suture in UCM 55499 is much shallower than those of larger tyrannosaurid individuals (e.g., Voris et al., 2020; Yun, 2020, 2022). In summary, both small size and presence of multiple immature characters in UCM 55499 strongly indicate the juvenile status of the individual this specimen represents.

While it can be confidently stated that UCM 55499 originates from a small juvenile, this individual was probably more mature than some of the youngest tyrannosaurids described so far. Aside from embryonic material (Funston et al., 2021), these are the two-year-old *Tyrannosaurus rex* LACM 28471 (Erickson et al., 2004; Carr, 2020) and the two-to three-year-old *Tarbosaurus bataar* MPC-D 107/07 (Tsuihiji et al., 2011). In these specimens, the postorbital buttress is not clearly separated from the caudal shelf (Tsuihiji et al., 2011; Carr, 2020), whereas these

structures are well-separated in UCM 55499 like in more mature tyrannosaurids. Furthermore, the sagittal crest is either not present (Tsuihiji et al., 2011) or present only as a low ridge (Carr, 2020) in MPC-D 107/07 and LACM 28471, respectively, but is well-developed in UCM 55499. Lastly, the frontals of LACM 28471 and MPC-D 107/07 are considerably smaller than UCM 55499 (Currie, 2003a; Carr & Williamson, 2004; Tsuihiji et al., 2011). Therefore, it is reasonable to assume that UCM 55499 belonged to an individual that was more ontogenetically mature than LACM 28471 and MPC-D 107/07.

Implications for ontogeny of *Daspletosaurus horneri*:

As mentioned above, UCM 55499 probably represents *Daspletosaurus horneri*, and its small size as well as the presence of a suite of immature characters suggest its juvenile status. Currie (2003b)'s allometric equation relating frontal width (FW) to frontal length (FL) in tyrannosaurines ($\text{Log FL} = 0.507 * \text{Log FW} + 1.1523$, $R^2 = 0.8313$) indicates that the length of UCM 55499 was likely about 95.5 mm when the bone was complete. This estimated length, as well as the directly measurable depth and width of UCM 55499, are comparable to the corresponding dimensions of some juvenile tyrannosaurid specimens such as CMNH 7541 and TMP 1994.143.0001, which have skull lengths of about 575 mm and 620 mm, respectively (Currie, 2003a). Within the growth series of *Daspletosaurus horneri* initially reported by Carr et al. (2017), the skull length of the individual represented by the smallest juvenile dentary specimen (MOR 553S/7.19.0.97) was estimated as slightly more than 496 mm. The next smallest individual in the sample, represented by the partial maxilla AMNH FARB 5477, is either a large juvenile (Carr et al., 2017) or a small subadult (Delcourt, 2017), and has a maxillary tooth row about 384.2 mm long. An equation of Currie (2003b) that relates maxillary tooth row length (MTR) to skull length (SKL) in tyrannosaurines ($\text{Log SKL} = 0.98 * \text{Log MTR} + 0.40$, $R^2 = 0.96$) estimates the complete skull length for this specimen to be about 848 mm. Therefore, UCM 55499 is important in being one of the few known examples of juvenile *Daspletosaurus horneri* (Carr et al., 2017; Voris et al., 2019), and potentially represents an intermediate growth stage between the previously described smallest juvenile and the next smallest available specimen.

Previously, the only known frontals of *Daspletosaurus horneri* were those of MOR 590 and MOR 1130, respectively a large subadult and an adult (Carr et al., 2017). As both of these specimens have been described only briefly (Carr et al., 2017), investigating ontogenetic variation in the frontal of *Daspletosaurus horneri* is difficult. Nevertheless, several preliminary inferences can be made, based on the available information.

Frontals of large *Daspletosaurus horneri* individuals are like those of similarly-sized *Daspletosaurus torosus*, and of derived tyrannosaurines such as *Tyrannosaurus rex*, in having a narrow nasal process, an elongated and tall sa-

gittal crest, and a transversely expanded body with a roughly quadrangular outline (e.g., Carr, 1999; Currie, 2003a; Carr & Williamson, 2004; Lehman & Wick, 2013; Carr et al., 2017; Yun, 2020). The nasal process of UCM 55499 was presumably wide, based on the width of the area preserved medial to the joint surface for the prefrontal. An ontogenetic transition from a wide to a narrow nasal process of the frontal has been reported in *Tyrannosaurus rex* (Carr & Williamson, 2004; Carr, 2020). The sagittal crest of UCM 55499 is elongated and likely was tall. Such an elongated and tall sagittal crest is present in similarly-sized juvenile *Tyrannosaurus rex* (Carr, 1999, 2020; Carr & Williamson, 2004). While the postorbital buttress and the caudal shelf of UCM 55499 are separated from each other and extend laterally (Figs. 1A, 2A), they are obviously not expanded to the degree seen in large tyrannosaurines (Currie, 2003a; Carr & Williamson, 2004; Lehman & Wick, 2013; Yun, 2020). The caudal margin of the lacrimal socket of UCM 55499 is transversely narrow in dorsal view, and this reflects the minimally expanded shape of the bone as well (e.g., Carr, 1999; Carr & Williamson, 2004; Yun, 2020, 2022). These characters are also shared with a similarly-sized juvenile specimen (CMNH 7541) of *Tyrannosaurus rex* (Carr, 1999; Carr & Williamson, 2004). The “forehead” region in UCM 55499 is flat, unlike the concave condition that slopes towards the interfrontal suture in adult *Daspletosaurus horneri* (Carr et al., 2017; Voris et al., 2020, 2022). Transition from flat to medioventrally concave condition in this region has been reported in *Tyrannosaurus rex* (Carr, 1999, 2020). Lastly, the cerebral fossa in UCM 55499 is well-defined and deep, unlike the relatively shallow condition in larger tyrannosaurid frontals (Carr, 2020; Yun, 2020, 2022). Ontogenetic transition between deep to shallow cerebral fossa is present in *Tyrannosaurus rex* (Carr, 2020). Intriguingly, a similar ontogenetic variation is present in ornithischian dinosaur *Psittacosaurus*, and such change is likely due to increasing distance between the brain and the braincase during growth (Bullar et al., 2019).

Collectively, these features suggest that patterns of ontogenetic changes in the frontal of *Daspletosaurus horneri* were largely similar to those seen in *Tyrannosaurus rex*. However, UCM 55499 differs from the similarly-sized juvenile *Tyrannosaurus rex* (CMNH 7541) in at least one respect, as the orbital slot in the former is a subvertical groove (Figs. 1D, 2D) similar to larger tyrannosaurids (Currie, 2003a; McDonald et al., 2018; Yun, 2020, 2022), but in the latter it is a shallow slot with a relatively elongated margin (Carr, 1999, 2020). A shallow orbital slot with an elongate margin is a plesiomorphic feature in tyrannosauroids (e.g., Tsuihiji et al., 2012) and can be seen in young individuals of tyrannosaurids (e.g., Carr, 1999, 2020; Tsuihiji et al., 2011; Bever et al., 2013). This indicates that the derived state of this character (i.e., subvertical groove-like slot) may have developed earlier in ontogenetic growth in *Daspletosaurus horneri* than in *Tyrannosaurus rex*. Of note, Voris et al. (2022) found

that major cranial ontogenetic changes in *Gorgosaurus libratus* occurred at smaller body size and younger age compared to the larger *Tyrannosaurus rex*. Given that the adult body size of *Daspletosaurus horneri* is similar to that of *Gorgosaurus libratus* (Carr et al., 2017), the difference in morphology of the orbital slot between CMNH 7541 and UCM 55499 may also potentially be due to similar reason.

Large individuals of *Daspletosaurus horneri* have a broad, teardrop-shaped prefrontal in dorsal part of the skull (Carr et al., 2017: fig. 1F), like other members of the same genus (Voris et al., 2020). The dorsal part of the preserved joint surface for the prefrontal in UCM 55499 is narrow and groove-like (Figs. 1C, 2C), which suggests that the prefrontal would have been only narrowly exposed on the skull roof. Carr (2020) noted an ontogenetic shift in *Tyrannosaurus rex* from a narrow joint surface for the prefrontal to a wide one. Therefore, the morphology of this feature in UCM 55499 implies that *Daspletosaurus horneri* exhibited an ontogenetic change in this character similar to that seen in *Tyrannosaurus rex*. However, identification of this possible ontogenetic variation should be considered provisional, as significant individual variation exists in tyrannosaurids with regard to the degree of exposure of the prefrontal, including its occasional fusion to the adjacent bones (e.g., Brochu, 2003; Currie, 2003a; Bever et al., 2013).

Another potential ontogenetic variation involves the orientation of the dorsotemporal ridge. The ridge in UCM 55499 is sinuous, just as in larger specimens of *Daspletosaurus horneri* (Carr et al., 2017), but differs from these in having a mediolateral orientation (Figs. 1A, 2A) rather than a rostralateral one (Voris et al., 2020). Ontogenetic variation in this feature is present in *Tyrannosaurus rex* (Carr, 2020). It is noteworthy, however, that some tyrannosaurids, like *Daspletosaurus torosus* and *Tyrannosaurus rex*, show individual, non-ontogenetic variation in the orientation of the dorsotemporal ridge (Carr et al., 2017; Voris et al., 2020). Additional discoveries of more *Daspletosaurus horneri* specimens representing different growth stages will be necessary to determine whether true ontogenetic variation in this feature is present in this taxon.

CONCLUSIONS

The specimen UCM 55499 represents a left juvenile tyrannosaurine frontal from the Two Medicine Formation of Montana, and is probably referable to *Daspletosaurus horneri*. This specimen is important for filling a size gap between small juvenile and large juvenile/small subadult stages in previously reported growth series of *Daspletosaurus horneri* (Carr et al., 2017; Delcourt, 2017), and also represents the first juvenile frontal documented for this taxon. Additionally, comparisons between UCM 55499 and frontals of other tyrannosaurids, including larger examples of *Daspletosaurus horneri*, indicate that despite some minor differences, ontogenetic changes in

the frontal bone of *Daspletosaurus horneri* were similar to those reported in other tyrannosaurids, such as *Tyrannosaurus rex*.

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