



A SUBADULT FRONTAL OF *DASPLETOSAURUS TOROSUS* (THEROPODA: TYRANNOSAURIDAE) FROM THE LATE CRETACEOUS OF ALBERTA, CANADA WITH IMPLICATIONS FOR TYRANNOSAURID ONTOGENY AND TAXONOMY

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ABSTRACT

An isolated frontal bone of *Daspletosaurus torosus* (Theropoda: Tyrannosauridae) is described which was probably found in the Dinosaur Park Formation (Upper Cretaceous) of Dinosaur Provincial Park, Alberta (Canada). It is important in terms of the first detailed osteological description of the frontal of *Daspletosaurus torosus*. The size and anatomical details of the specimen indicates the frontal belongs to a large subadult individual. This subadult frontal suggests that although ontogeny of *Daspletosaurus torosus* was generally similar to that of *Tyrannosaurus rex*, there were some distinct differences. Finally, certain features of this frontal bone indicate that some autapomorphies that have recently suggested for some tyrannosaurid taxa are inadequate due to their broad distribution within a clade.

INTRODUCTION

Tyrannosaurid theropods, which dominated terrestrial ecosystems of western North America and Asia during the Late Cretaceous as apex predators (Holtz, 2004; Brusatte *et al.*, 2010), represent the most iconic non-avian dinosaurs of all time. The members of this group are characterized by large, deep skulls with robust teeth, short forelimbs with two functional digits, and elongate hindlimbs with adaptations for cursorial behavior (Brochu, 2003; Holtz, 2004). Tyrannosauridae is highly diverse in cranial and skeletal morphology, however, as it includes relatively small-sized taxa with longirostrine skulls (Brusatte *et al.*, 2012; Lü *et al.*, 2014), medium-sized taxa with short snouts (Carr *et al.*, 2011; Loewen *et al.*, 2013) and very large taxa with robust skulls (Brochu, 2003; Holtz, 2004; Hone *et al.*, 2011; Yun, 2017; Persons *et al.*, 2019). As a result, tyrannosaurids have been included in many paleobiological studies related to systematics (*e.g.*, Loewen *et al.*, 2013; Carr *et al.*, 2017), ecological behavior (*e.g.*, Holtz, 2008), as well as paleodiversity and anatomy (*e.g.*, Carr, 1999; Currie, 2003; Carr & Williamson, 2004). Indeed, tyrannosaurid theropods are particularly important in understanding dinosaur paleobiology and Mesozoic terrestrial ecosystems as they represent advanced, bird-like coelurosaurian theropods, yet morphologically divergent from closely related lineages (Brusatte *et al.*, 2010; Yun, 2016; Carr *et al.*, 2017; Persons *et al.*, 2019).

Daspletosaurus is a genus of tyrannosaurid theropod erected by Russell (1970), which include the type species *Daspletosaurus torosus*, from the Oldman and Dinosaur Park Formations of Alberta and the referred species *Daspletosaurus horneri* from the Two Medicine Formation of Montana (Currie, 2003; Carr *et al.*, 2017). Unfortunately, despite the large numbers of individuals that have been mentioned (Currie, 2003) most of the referred specimens of *Daspletosaurus torosus* have not been properly described. This is especially true of juveniles and subadult individuals, as the majority of currently known *Daspletosaurus torosus* individuals are adults (Delcourt, 2017; Voris *et al.*, 2019). Currie (2003) only briefly described several *Daspletosaurus* specimens in his review on tyrannosaurid cranial anatomy, and the frontal element of juvenile *Daspletosaurus torosus* he had figured (TMP 1994.143.1) is now known as the misidentified *Gorgosaurus libratus* (Voris *et al.*, 2019). In summary, little is known about the morphological changes that occurred during the ontogeny of this species, and many questions remain unresolved. Thus, the present paper describes an isolated tyrannosaurid frontal bone (SDNHM 32701) from the Dinosaur Park Formation of southern Alberta that is assignable to *Daspletosaurus torosus* in an attempt to contribute to clarifications of these questions and problems. Although, admittedly, the specimen is fragmentary, it provides several informative anatomical features that are hard to observe in articulated specimens nonetheless. Furthermore, the discovery of this specimen is historically significant, as SDNHM 32701 predates the discovery of holotype in 1921 and naming of the *Daspletosaurus torosus* (Russell, 1970).

INSTITUTIONAL ABBREVIATIONS

CMN: Canadian Museum of Nature, Ottawa, Canada

LACM: Los Angeles County Museum, California, U.S.A.

SDNHM: San Diego Natural History Museum, San Diego, U.S.A.

TMP: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada

UMNH: Utah Museum of Natural History, Utah, U.S.A.

GEOLOGICAL SETTING

The specimen was purchased by San Diego Natural History Museum from Charles H. Sternberg in 1921. It was collected below Steeveville, Red Deer River of Alberta which is within the boundaries of what is now Dinosaur Provincial Park. Unfortunately, no additional information was provided. In the Park area, both Oldman Formation and Dinosaur Park Formation are exposed (Eberth & Evans, 2011). However, it is probable that this was collected from the Dinosaur Park Formation as Sternberg collected dinosaurs exclusively from this formation during the 1910s (Currie, 2005). Of note, Currie (2003) listed SDNHM 32701 as coming from the Dinosaur Park Formation as well, but he gave no reason for it. It is possible that the specimen was collected in 1917, as there are records that imply that Sternberg sold fossils that he collected in that year to San Diego Natural History Museum (Currie, 2005). If this assumption is correct, it is likely that it was collected from the south side of the Red Deer River as Sternberg investigated this area in 1917 (Currie, 2005). Considering that Sternberg found dinosaur taxa (*e.g.*, *Centrosaurus*, *Corythosaurus*) that are exclusive in lower or middle part of the formation in this area (*e.g.*, Arbour *et al.*, 2009; Eberth & Evans, 2011; Fowler, 2017), it is probable that the specimen that is described in this paper came from either one of these stratigraphic positions instead. This is further supported by the taxonomic identity of the specimen, *Daspletosaurus torosus*, and certain materials of this taxon have been only recovered in the lower two-thirds of the Dinosaur Park Formation (Carr *et al.*, 2017).

The Dinosaur Park Formation is approximately 75 m thick. The sediments composing it were derived from the erosion of western mountains and deposited during the initial stages of the last major transgression of the Western Interior Seaway (Eberth, 2005; Fowler, 2017). ⁴⁰Ar / ³⁹Ar radiometric dating constrains the age of the Dinosaur Park Formation to between 77.3 Ma (the uppermost part of the Oldman Formation) and 75.46 Ma (the base of Bearpaw Formation) (Fowler, 2017). Given that the sedimentation rates for the upper 22 meters of the Dinosaur Park Formation and Bearpaw Formation transition were slow (Carr *et al.*, 2017), the top of the Dinosaur Park Formation is likely slightly older than 75.46 Ma. The formation is famous for the rich abundance of vertebrate fossils including fishes, amphibians, turtles, squamates, crocodiles, pterosaurs, dinosaurs and mammals (*e.g.*, Currie & Koppelhus, 2005; Longrich, 2008). The Dinosaur Park Formation is partly equivalent in age and partly correlates with the Campanian deposits in Montana such as Judith River Formation (Eberth, 1997).

MATERIAL AND METHODS

Due to the lack of funding at the beginning of this project, this anatomical study was conducted using high-quality casts of the original specimen housed at the San Diego Natural History Museum (SDNHM 32701) made through 3D scanning. Anatomical comparisons were made with other North American tyrannosauroids such as *Bistahieversor* and tyrannosaurids. The comparisons were made through an extensive review on the literature and direct observations on several casts. The anatomical nomenclature used in this study follows Currie (2003), Carr *et al.* (2017) and McDonald *et al.* (2018).

SYSTEMATIC PALEONTOLOGY

Tyrannosauroidea Osborn, 1906

Tyrannosauridae Osborn, 1906

Tyrannosaurinae Osborn, 1906

Daspletosaurini Voris *et al.*, 2020 [in press]

Daspletosaurus Russell, 1970
Daspletosaurus torosus Russell, 1970

MATERIAL

SDNHM 32701. An incomplete right frontal bone, lacking the rostral end of the nasal process, most of the sagittal crest and caudolateral parts of the bone.

LOCALITY AND AGE

Dinosaur Provincial Park, Alberta, Canada. Upper Cretaceous (Campanian) Dinosaur Park Formation.

ASSIGNMENT

Currie (2003) listed SDNHM 32701 as *Daspletosaurus* sp., but did not give a reason for this referral. The specimen can be unambiguously referred as *Daspletosaurus* based on the presence of one autapomorphy of the genus: the presence of rostrocaudal ridge that is present along the nasal process of the frontal (Carr *et al.*, 2017; Voris *et al.*, 2019; 2020 [in press]). The specimen can also be identified as a tyrannosaurine, in which *Daspletosaurus torosus* is the only known example from the Dinosaur Park Formation (Carr *et al.*, 2017) based on the presence of narrow nasal process, wide lacrimal socket, elongate and tall sagittal crest, and deep rostral part of postorbital suture (Carr & Williamson, 2004; Carr *et al.*, 2017; Voris *et al.*, 2020 [in press]). Lastly, SDNHM 32701 differs from *Daspletosaurus horneri*, but is similar to *Daspletosaurus torosus*, in having a straight dorsotemporal ridge (*cf.* Carr *et al.*, 2017). In summary, details in anatomy and its stratigraphic position suggests SDNHM 32701 is assignable to *Daspletosaurus torosus*.

Of note, the taxonomy of *Daspletosaurus* specimens from the Dinosaur Park Formation is controversial: while the majority of the recent studies have assigned these specimens as *Daspletosaurus torosus* (*e.g.*, Carr, 1999; Carr *et al.*, 2017; Voris *et al.*, 2019; 2020 [in press]; Yun, 2020a, b), some studies have referred to them as unnamed, different species (*e.g.*, Currie, 2003; Delcourt, 2017). Here, the classification that considers Dinosaur Park *Daspletosaurus* as *torosus* is adopted given that there is a high possibility that the holotype of *Daspletosaurus torosus* is in fact from the Dinosaur Park Formation (as explained above) and not from the Oldman Formation as originally suggested (Carr, T.D. pers. comm.).

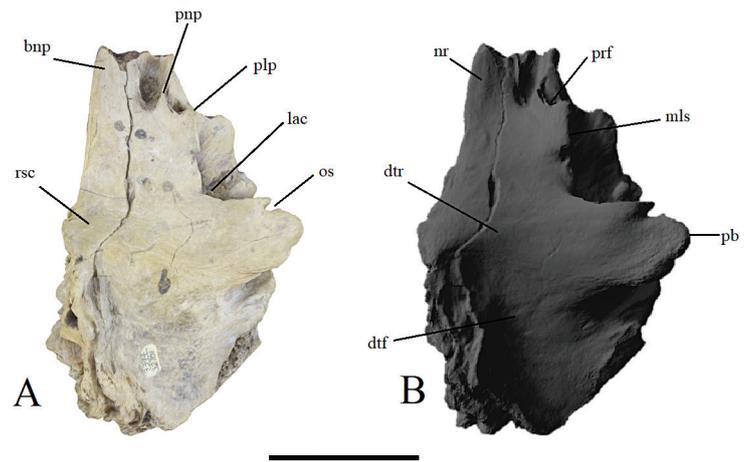
COMPARATIVE DESCRIPTION

The isolated right frontal, SDNHM 32701, is well preserved except for some minor parts that eroded away (Fig. 1). When measured in a manner described by Currie (2003), the length (126 mm), width (67 mm) and depth (41 mm) are comparable to large individuals of *Albertosaurus*, *Gorgosaurus* and *Daspletosaurus* based on the specimens measured and indexed by Currie (2003). The ratio of depth to width is 0.61, comparable to frontals of subadult and adult tyrannosaurines (Currie, 2003; McDonald *et al.*, 2018). In this description, the morphology of SDNHM 32701 is divided into six sections, detailing the dorsal, lateral, medial, ventral, rostral, and caudal surfaces.

Dorsal Surface

Only a basal part of the nasal process is preserved in SDNHM 32701 (Fig. 1). It is narrow in width, which is typical for large tyrannosaurines like *Daspletosaurus* and *Tyrannosaurus* (Carr & Williamson, 2004; Lehman & Wick, 2012). The dorsal surface of this process bears a ridge that is rostrocaudally extending along the process (Fig. 1B), a feature that characterizes both species (*D. torosus*, *D. horneri*) of *Daspletosaurus* (Carr *et al.*, 2017). Lateral to this process, there is

Figure 1. A) SDNHM 32701 and B) 3D-model in dorsal view. Abbreviations: *bnp*, basal of nasal process; *dtf*, dorsotemporal fossa; *dtr*, dorsotemporal ridge; *lac*, lacrimal socket; *mls*, medial part of lacrimal socket; *os*, orbital slot; *pb*, postorbital buttress; *plp*, prefrontolacrimal process; *pnp*, prefrontonasal process; *prf*, joint surface for prefrontal; *rsc*, rostral part of sagittal crest. Scale bar equals 50 mm. Images and 3D model of the specimen are courtesy of San Diego Natural History Museum.



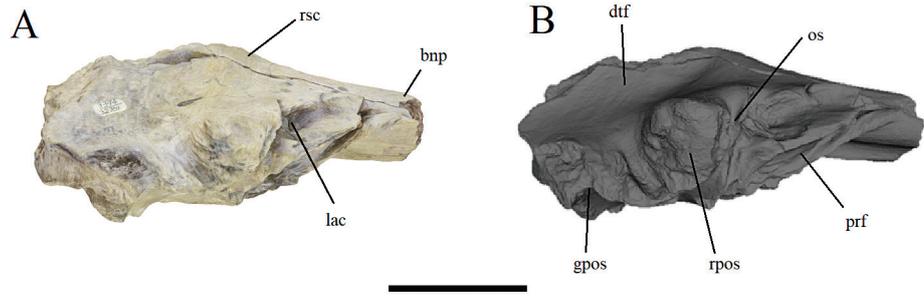
a deep, narrow and tear-drop shaped depression for the caudolateral process of the nasal (Fig. 1), indicating the these processes in this individual were narrow, as in the holotype (CMN 8506) of *Daspletosaurus torosus* (Carr & Williamson, 2004: Fig. 8). Lateral to this depression, there is a short, triangular and rostrally facing prefrontonasal process, which is only slightly separated from the similarly shaped prefrontolacrimal process by a slight notch, although the latter is slightly broken (Fig. 1). Similar configurations are present in the holotype (UMNH VP 28348) of “*Dynamoterror*” (McDonald *et al.*, 2018) and one specimen (TMP 80.16.924) of *Daspletosaurus torosus* (Lehman & Wick, 2012: Fig. 11, mislabeled as *Gorgosaurus*). In other specimens of *Daspletosaurus torosus* (CMN 8506, TMP 2001.36.1), the two processes are widely separated (Carr & Williamson, 2004: Fig. 8; Voris *et al.*, 2020 [in press]: Fig. 8B). The subcutaneous surface of the forehead region (*sensu* Carr & Williamson, 2004) swells caudodorsally, although it is generally flattened. The dorsomedial surface is raised and rounded, which is the rostral part of the sagittal crest (Fig. 1). This part is slightly positioned rostrally to the medial part of the dorsotemporal ridge (Fig. 1B), and similar condition is reported from the holotype (TMP 2010.5.7) of “*Thanatotheristes*” *degrootorum* (Voris *et al.*, 2020 [in press]; see below on the status of this taxon). Although the rostral margin of dorsotemporal fossa is indistinct in SDNHM 32701, the form of the medial part of dorsotemporal ridge indicates the margin is straight as in other specimens of *Daspletosaurus torosus* (Carr *et al.*, 2017). The dorsotemporal fossa is covered with slight grooves that extend mediolaterally (Fig. 1B), and its medial surface strongly curves dorsally (Figs. 5, 6). This curvature of the bone grain indicates that the present specimen had a very tall sagittal crest, as in other derived tyrannosaurines (Carr *et al.*, 2017).

There is a deep, rostrally facing lacrimal socket in the rostromedial corner (Fig. 1A), and the medial margin of this socket is rostrocaudally elongated (Fig. 1B) as in albertosaurines and immature tyrannosaurines (Carr & Williamson, 2004; 2010). This elongated margin suggests that SDNHM 32701 belongs to a subadult individual. The caudal margin of the socket is mediolaterally wide, as in derived tyrannosaurines (Carr & Williamson, 2004). Lateral to the lacrimal socket is an orbital slot that would have separated the lacrimal and postorbital in an articulated skull (Fig. 1A). Caudal to this slot, a pronounced buttress for the articulation with the rostral part of the postorbital is present.

Lateral Surface

In lateral view, the groove-shaped joint surface for the prefrontal is positioned rostroventral to the lacrimal socket, and the central region of the surface is gener-

Figure 2. A) SDNHM 32701 and B) 3D-model in lateral view; Abbreviations: bnp, basal of nasal process; dtf, dorsotemporal fossa; gpos, groove between rostral and caudal parts of postorbital suture; lac, lacrimal socket; os, orbital slot; prf, joint surface for prefrontal; rpos, rostral part of the postorbital suture; rsc, rostral part of sagittal crest. Scale bar equals 50 mm. Images and 3D model of the specimen are courtesy of San Diego Natural History Museum.



ally smooth, albeit some subtle ridges are present (Fig. 2B). This contrasts with the condition in subadult *Tyrannosaurus* (LACM 23845), in which the surface is coarsened with low papillae and ridges (Carr & Williamson, 2004).

Laterally, the lacrimal socket progressively deepens caudally, while the caudal part of the socket is concealed by the postorbital buttress in lateral view (Fig. 2A). The orbital slot that separates the lacrimal and postorbital sutures is groove-like, and steeply extends dorsolaterally (Fig. 2B) as in other specimens of *Daspletosaurus torosus* (Carr *et al.*, 2017). Caudal to this slot, the rostral part of the postorbital suture is present (Fig. 2B). The depth of this part is 28 mm, comparable with the holotype (TMP 2010.5.7) of “*Thanatotheristes*” *degrootorum* while much deeper than those of albertosaurines and *Teratophoneus* (Voris *et al.*, 2020 [in press]). The texture of this suture is bulbous and coarse, marked by deep ridges (Fig. 2) as in large tyrannosaurid specimens (Carr & Williamson, 2004).

Although the caudal part of the postorbital suture is broken, a medial part of the groove that separates the rostral and caudal parts of the postorbital suture is present and visible in lateral view (Fig. 2B). This groove is probably homologous with the deep groove in “*Dynamoterror*” and *Teratophoneus* (McDonald *et al.*, 2018; Yun, 2020b), open foramen that penetrates into the skull roof in *Tyrannosaurus* (Brochu, 2003; Lehman & Wick, 2012), and small neurovascular foramen in the orbital wall in an unnamed tyrannosaurine from the Aguja Formation of Texas (Lehman & Wick, 2012). The orbital wall is exposed medioventrally to the postorbital suture, and is visible laterally (Fig. 2).

In lateral view, the rostralmost part of the sagittal crest is visible rostral to the dorsotemporal ridge (Fig. 2A) as reported in “*Thanatotheristes*” *degrootorum* (Voris *et al.*, 2020 [in press]).

Medial Surface

The medial surface of SDNHM 32701 is nearly occupied entirely by the interfrontal suture. The rostral part of the suture is nearly flat, vertical and covered with a series of slight, rostrally opening U-shaped ridges. In the middle part of the suture, the ridges are straighter and much more distinct (Fig. 3B). Ventral parts of caudal part of the nasal cavity and olfactory bulb fossa are exposed and visible in medial view (Fig. 3A).

Figure 3. A) SDNHM 32701 and B) 3D-model in medial view. Abbreviations: cnc, caudal extent of nasal cavity; ifs, interfrontal suture; obf, olfactory bulb fossa; rsc, rostral part of sagittal crest. Scale bar equals 50 mm. Images and 3D model of the specimen are courtesy of San Diego Natural History Museum.

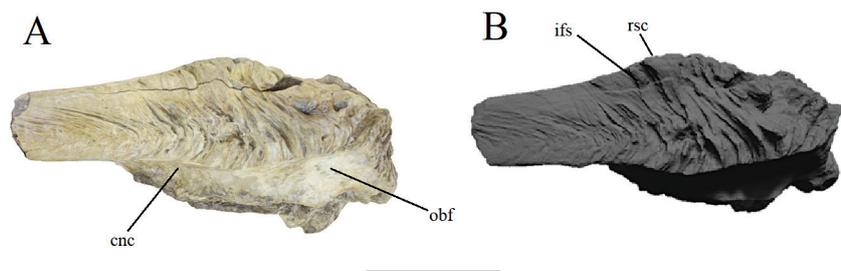
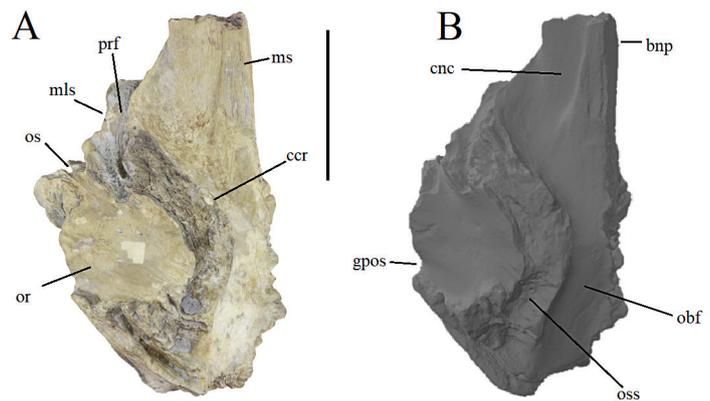


Figure 4. A) SDNHM 32701 and B) 3D-model in ventral view. Abbreviations: *bnp*, basal of nasal process; *ccr*, crista cranii; *cnc*, caudal extent of nasal cavity; *gpos*, groove between rostral and caudal parts of postorbital suture; *mls*, medial part of lacrimal socket; *ms*, median septum; *obf*, olfactory bulb fossa; *or*, orbit; *os*, orbital slot; *oss*, orbitosphenoid suture; *prf*, joint surface for prefrontal. Scale bar equals 50 mm. Images and 3D model of the specimen are courtesy of San Diego Natural History Museum.



Ventral Surface

In the rostromedial part of the ventral surface, there is a narrow, distinct median septum that widens caudally (Fig. 4A). The distinct nature of bone strongly differs from that of *Alioramus*, which is very indistinctly developed (Bever *et al.*, 2013: Fig. 9) but similar to those in *Gorgosaurus* individuals and subadult *Tyrannosaurus* (Currie, 2003: Fig. 20B; Carr & Williamson, 2004: Fig. 15E; Ali *et al.*, 2008: Fig. 1A). A longitudinal groove is present at the middle of this septum (Fig. 4B). Laterally, there is a deep concave fossa that forms the caudal part of the nasal cavity, and the deepest portion is positioned at the middle (Fig. 4B).

The crista cranii is thick, rugose and crescent shaped (Fig. 4), unlike the straight conditions in *Alioramus* and *Aguja tyrannosaurine* (Lehman & Wick, 2012: Fig. 4D; Bever *et al.*, 2013: Fig. 9) but similar to those in *Gorgosaurus*, *Nanuqsaurus*, “*Thanatotheristes*” and subadult *Tyrannosaurus* (Carr & Williamson, 2004: Fig. 15E; Ali *et al.*, 2008: Fig. 1A; Fiorillo & Tykoski, 2014: Fig. 4D; Voris *et al.*, 2020 [in press]: Fig. S5A). The ethmoid scar is only weakly developed, as is typical for tyrannosaurids (Bever *et al.*, 2013: Fig. 9; McDonald *et al.*, 2018).

The contact surface for the prefrontal is situated at the rostromedial corner of the ventral surface, and is relatively broad and complex (Fig. 4A). This morphology is present in other *Daspletosaurus torosus* specimens as well (Voris *et al.*, 2020 [in press]). The orbital wall is a wide, teardrop-shaped fossa (Fig. 4A) a condition that is largely similar to those in other derived tyrannosaurines (Lehman & Wick, 2012: Fig. 4D; McDonald *et al.*, 2018: Fig. 3A). The orbitosphenoid suture is positioned caudomedial to the orbital wall (Fig. 4B) and it is a subcircular concavity that faces medioventrally. The olfactory bulb fossa is large, teardrop-shaped, and its mediolateral axis is strongly angled dorsolaterally (Fig. 4B).

Rostral Surface

The medialmost part of the rostral surface is the rostrally projecting base of the nasal process (Fig. 5A). The base is narrow when observed in rostral view, as in other large tyrannosaurines (Lehman & Wick, 2012). Lateral to this is a marked, round depression for the caudolateral process of the nasal (Fig. 5B). Caudolateral to this depression, a short, triangular prefrontonasal process is present and laterally, a slightly broken, similarly shaped prefrontolacrimal process is present. A short prefrontolacrimal process is typical for all tyrannosaurids except for *Teratophoneus* and *Nanuqsaurus* (Fiorillo & Tykoski, 2014). Rostrally, the two processes are separated from each other by a small notch, which marks the location of prefrontal exposure on the skull roof (*cf.* McDonald *et al.*, 2018). The ventral part of the joint surface for the prefrontal is arched dorsomedially, as in “*Thanatotheristes*” and *Daspletosaurus* (Voris *et al.*, 2020 [in press]).

Figure 5. A) SDNHM 32701 and B) 3D-model in rostral view. Abbreviations: *bnp*, basal of nasal process; *lac*, lacrimal socket; *os*, orbital slot; *plp*, prefrontolacrimal process; *pnp*, prefrontonasal process; *prf*, joint surface for prefrontal; *rsc*, rostral part of sagittal crest. Scale bar equals 50 mm. Images and 3D model of the specimen are courtesy of San Diego Natural History Museum.

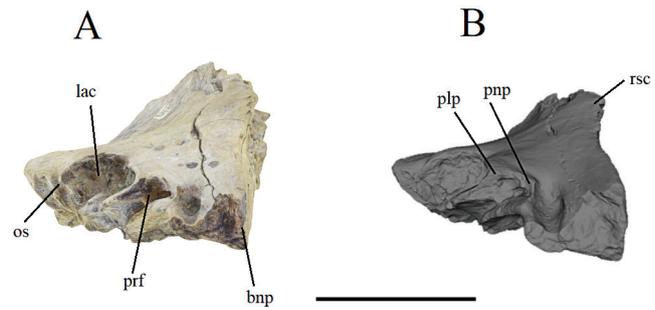
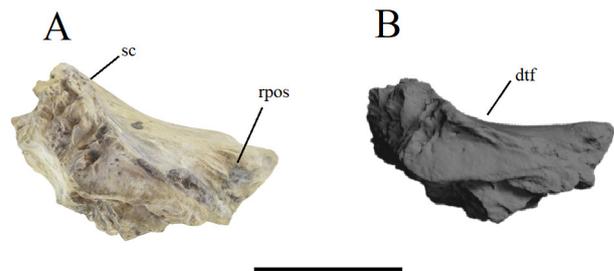


Figure 6. A) SDNHM 32701 and B) 3D-model in caudal view. Abbreviations: *dtf*, dorsotemporal fossa; *rpos*, rostral part of the postorbital suture; *sc*, sagittal crest. Scale bar equals 50 mm. Images and 3D model of the specimen are courtesy of San Diego Natural History Museum.



The caudalmost portion of the lacrimal socket is observable in rostral view. It is a wide, cup-shaped socket that is facing rostrally (Fig. 5A), which is comparable to *Gorgosaurus*, *Daspletosaurus* and some specimens of *Tyrannosaurus* (Currie, 2003) but differs from *Nanuqsaurus* in which the lacrimal socket is taller than wide (Fiorillo & Tykoski, 2014: Fig. 4E). The groove for the orbital slot and rostral surface of the postorbital buttress is positioned lateral to this socket (Fig. 5). In rostral view, the rostral portion of the sagittal crest strongly rises dorsally (Fig. 5B).

Caudal Surface

In caudal view, a deep, dorsolaterally oriented dorsotemporal fossa is well visible (Fig. 6B). The strongly concave, dorsally sloping dorsotemporal fossa indicates that a very tall sagittal crest was originally present in this individual, as in other derived tyrannosaurines (Carr *et al.*, 2017).

The lateralmost part of the caudal surface is the rostral part of the postorbital suture, which is marked by deep ridges and grooves (Fig. 6A).

DISCUSSION

Implications on the Ontogeny of Daspletosaurus torosus

The width between the interfrontal suture and lateralmost part of the postorbital buttress of SDNHM 32701 is approximately 71% of that of a large adult specimen of *Daspletosaurus torosus* (TMP 2001.36.1; taken from Voris *et al.*, 2020 [in press]: Fig. 8B), in which the skull length is about 1060 mm (Voris *et al.*, 2019). Scaling from the frontal width and skull length of TMP 2001.36.1 with a size about 9 m assumed for adult *Daspletosaurus*, this returns a body size about 6.39 m with a skull length of about 752.6 mm for an individual that SDNHM 32701 represents. Additionally, SDNHM 32701 shows several immature characters, including an elongate medial margin of the lacrimal socket and an indistinct rostral margin of the dorsotemporal fossa (Carr & Williamson, 2004). Thus, the size and details in anatomy suggest SDNHM 32701 represents a large subadult individual. Given that the majority of the current fossil record of *Daspletosaurus torosus* is overwhelmed by large adults (Voris *et al.*, 2019), SDNHM 32701 is important in representing a clue about the changes that occurred between subadult and adult growth stages of this taxon.

The nasal process of SDNHM 32701 is transversely narrow, which is similar to adult individuals (Carr & Williamson, 2004) but differs from those of currently known examples of juvenile tyrannosaurine, which all bear broad nasal processes (e.g., Carr, 1999: Fig. 6B; Carr & Williamson, 2004: Fig. 2A; Sereno *et al.*, 2009: Fig. 1B; Tsuihiji *et al.*, 2011: Fig. 5E). This suggests that in *Daspletosaurus torosus* constriction in nasal process width occurred during the juvenile-subadult growth phase. Similar ontogenetic dimorphism is found in *Tyrannosaurus* (Carr & Williamson, 2004). In SDNHM 32701, the prefrontonasal and prefrontolacrimal processes are in close proximity, which differs in adults as the two processes are widely separated (Voris *et al.*, 2020 [in press]: Fig. 8B). This suggests that in *Daspletosaurus torosus*, separation of these two processes occurred between the subadult and adult growth stages. Such unique ontogenetic dimorphism has not been reported for other tyrannosaurids and could be unique for *Daspletosaurus torosus*.

The medial margin of the lacrimal socket in SDNHM 32701 is rostrocaudally elongate as in immature tyrannosaurids (Carr, 1999; Carr & Williamson, 2004), while the width of the caudal margin of the socket is transversely wide as in adult tyrannosaurines (Carr & Williamson, 2004). This suggests that in *Daspletosaurus torosus*, widening of the frontal has occurred earlier than the shortening of the lacrimal socket, and the latter probably occurred when the animal was close to maturity. This differs from the condition in *Tyrannosaurus*, as the similarly-sized subadult individual LACM 23845 already bears a short, but wide lacrimal socket (Currie, 2003; Carr & Williamson, 2004). Lastly, the rostral margin of dorsotemporal fossa is indistinct in SDNHM 32701 compared to adults (Voris *et al.*, 2020 [in press]: Fig. 8B) while the similarly-sized subadult *Tyrannosaurus* exhibits a distinct margin as in adults (Carr & Williamson, 2004: Fig. 15C).

Collectively, the morphology of SDNHM 32701 suggests that while the general pattern of frontal ontogeny in *Daspletosaurus torosus* is similar to that of *Tyrannosaurus*, at least some of the adult characters (e.g., short lacrimal socket, distinct rostral margin of dorsotemporal fossa) probably developed late in ontogeny when compared with *Tyrannosaurus*. These differences may reflect a presence of heterochrony in tyrannosaurid evolution but certainly, additional discoveries and descriptions of tyrannosaurid specimens of different growth stages are necessary to clarify this issue.

Implications for Tyrannosaurine Taxonomy

The anatomy of SDNHM 32701 bears several important implications for the taxonomy of Tyrannosaurinae, especially about originally proposed autapomorphies of recently erected taxa. In their original description of “*Dynamoterror dynastes*” (regarded as a nomen dubium here, following Yun, 2020b), McDonald *et al.* (2018) asserted that the close proximity of the prefrontonasal and prefrontolacrimal processes, which are separated by a shallow notch, is an unambiguous autapomorphy of this taxon. However, a nearly identical morphology is present in SDNHM 32701, and at least one other *Daspletosaurus torosus* specimen (TMP 80.16.924) also has a similar morphology (Lehman & Wick, 2012: Fig. 11). As aforementioned, this area may be in the subject of ontogenetic variation as well. Thus, this character is inadequate to diagnose a tyrannosaurine taxon.

Voris *et al.* (2020 [in press]: 3) proposed that two frontal characters are apomorphic for *Thanatotheristes degrootorum*, which are as follows: “sagittal crest on the frontal extends anterior to the supratemporal ridge as a broad and rounded ridge; lacrimal contact surface on the frontal extends anteromedially at -60° relative to the interfrontal suture”. However, the rostral part of the sagittal crest extends rostral to the dorsotemporal ridge in SDNHM 32701 as well, and a similar

feature is also present in an unnamed tyrannosaurine from the Aguja Formation as well (Lehman & Wick, 2012). Lastly, the angle between the interfrontal suture and the midpoint of the caudal margin of lacrimal socket is approximately 60° in SDNHM 32701. Thus, two proposed autapomorphies in the frontal of *Thanatotheristes degrootorum* are rejected. Additionally, known material of *Thanatotheristes degrootorum* are very similar to those of *Daspletosaurus* (Voris *et al.*, 2020 [in press]) and the number of currently known morphological differences between these two genera is actually fewer than those between two *Daspletosaurus* species, *D. torosus* and *D. horneri* (Carr *et al.*, 2017). Therefore, the genus name “*Thanatotheristes*” should be considered as a junior subjective synonym of *Daspletosaurus*.

Moreover, *Daspletosaurus degrootorum* may have even been an anagenetic ancestor of *Daspletosaurus torosus*. According to Carr *et al.* (2017), the primary criteria for the hypothesis of anagenesis include: (1) the taxa are sister species or a phylogenetically successive series; (2) the species are stratigraphically sequential; (3) the phylogenetic relationships do not conflict with stratigraphic sequence; (4) the species are from the same landmass. *Daspletosaurus degrootorum* is sister to an anagenetic lineage of two species of *Daspletosaurus*, and they are stratigraphically successive (Carr *et al.*, 2017; Voris *et al.*, 2020 [in press]). Lastly, fossils of both *Daspletosaurus degrootorum* and *Daspletosaurus torosus* are restricted in southern Alberta (Voris *et al.*, 2020 [in press]). The time gap that separated *D. degrootorum* and *D. torosus* exceeds that between *D. torosus* and *D. horneri* (Carr *et al.*, 2017; Voris *et al.*, 2020 [in press]) so obviously, testing for this hypothesis would require new discoveries of additional tyrannosaurid materials from the age between 90 and 80 Ma, when the origin and initial diversification of tyrannosaurids occurred (*e.g.*, Voris *et al.*, 2020 [in press]).

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REFERENCES

- Ali, F., D.K. Zelenitsky, F. Therrien & D.B. Weishampel. 2008. Homology of the ethmoid complex of tyrannosaurids and its implications for the reconstruction of the olfactory apparatus of non-avian theropods. – *Journal of Vertebrate Paleontology* 28: 123-133.
- Arbour, V.M., M.E. Burns, R.L. & Sissons. 2009. A redescription of the ankylosaurid dinosaur *Dyoplosaurus acutosquameus* Parks, 1924 (Ornithischia: Ankylosauria) and a revision of the genus. – *Journal of Vertebrate Paleontology* 29: 1117-1135.
- Bever, G.S., S.L. Brusatte, T.D. Carr, X. Xu, A.M. Balanoff & M.A. Norell. 2013. The braincase anatomy of the Late Cretaceous dinosaur *Alioramus* (Theropoda: Tyrannosauroida). – *Bulletin of the American Museum of Natural History* 376: 1-72
- Brochu, C.A. 2003. Osteology of *Tyrannosaurus rex*: Insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. – *Journal of Vertebrate Paleontology* 22(Supplement 4): 1-138.

- Brusatte, S.L., T.D. Carr & M.A. Norell. 2012. The osteology of *Alioramus*, a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. – *Bulletin of the American Museum of Natural History* 366: 1-197.
- Brusatte, S.L., M.A. Norell, T.D. Carr, G.M. Erickson, J.R. Hutchinson, A.M. Balanoff, G.S. Bever, J.N. Choiniere, P.J. Makovicky & X. Xu. 2010. *Tyrannosaur* paleobiology: new research on ancient exemplar organisms. – *Science* 329: 1481-1485.
- Carr, T.D. 1999. Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Theropoda). – *Journal of Vertebrate Paleontology* 19: 497-520.
- Carr, T.D. & T.E. Williamson. 2004. Diversity of late Maastrichtian Tyrannosauridae (Dinosauria: Theropoda) from western North America. – *Zoological Journal of the Linnean Society* 142: 479-523.
- Carr, T.D. & T.E. Williamson. 2010. *Bistahieversor sealeyi*, gen. et sp. nov., a new tyrannosauroid from New Mexico and the origin of deep snouts in Tyrannosauroida. – *Journal of Vertebrate Paleontology* 30: 1-16.
- Carr, T.D., T.E. Williamson, B.B. Britt K. & Stadtman. 2011. Evidence for high taxonomic and morphometric tyrannosauroid diversity in the Late Cretaceous (Late Campanian) of the American Southwest and a new short-skulled tyrannosaurid from the Kaiparowits formation of Utah. – *Naturwissenschaften* 98: 241-246.
- Carr, T.D., D.J. Varricchio, J.C. Sedlmayr, E.M. Roberts & J.R. Moore. 2017. A new *tyrannosaur* with evidence for anagenesis and crocodile-like facial sensory system. – *Scientific Reports* 7: 44942.
- Currie, P.J. 2003. Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. – *Acta Palaeontologica Polonica* 48: 191-226.
- Currie, P.J. 2005. History of research. In: Currie, P.J. & E.B. Koppelhus. Eds. *Dinosaur Provincial Park: A spectacular ancient ecosystem revealed*. – Bloomington, Indiana University Press: 3-33.
- Currie, P.J. & E.B. Koppelhus. 2005. *Dinosaur Provincial Park: A spectacular ancient ecosystem revealed*. – Bloomington, Indiana University Press.
- Delcourt, R. 2017. A subadult maxilla of a Tyrannosauridae from the Two Medicine Formation, Montana, United States. – *Papéis Avulsos de Zoologia* 57: 113-118.
- Eberth, D.A. 1997. Judith River Wedge. In: Currie, P.J. & K. Padian. Eds. *Encyclopedia of Dinosaurs*. – San Diego, Academic Press: 379-385.
- Eberth, D.A. 2005. The geology. In: Currie, P.J. & E.B. Koppelhus. Eds. *Dinosaur Provincial Park: A spectacular ancient ecosystem revealed*. – Bloomington, Indiana University Press: 54-82.
- Eberth, D.A. & D.C. Evans. 2011. Geology and palaeontology of Dinosaur Provincial Park, Alberta. – *Drumheller, Special Publication of the Royal Tyrrell Museum*.
- Fowler, D.W. 2017. Revised geochronology, correlation, and dinosaur stratigraphic ranges of the Santonian-Maastrichtian (Late Cretaceous) formations of the Western Interior of North America. – *PLoS ONE* 12: e0188426.
- Fiorillo, A.R. & R.S. Tykoski. 2014. A diminutive new *tyrannosaur* from the top of the world. – *PLoS ONE* 9: e91287.
- Holtz, T.R., Jr. 2004. Tyrannosauroida. In: Weishampel, D.B., P. Dodson & H. Osmolska. Eds. *The Dinosauria*. [Second Edition]. – Berkeley, University of California Press: 111-136.
- Holtz, T.R., Jr. 2008. A critical re-appraisal of the obligate scavenging hypothesis for *Tyrannosaurus rex* and other tyrant dinosaurs. In: Larson, P. & K.

- Carpenter. Eds. *Tyrannosaurus rex*: The tyrant king. – Bloomington, Indiana University Press: 370-396.
- Hone, D.W.E., W. Wang, C. Sullivan, X. Zhao, S. Chen, D. Li, S. Ji, Q. Ji & X. Xu. 2011. A new, large tyrannosaurine theropod from the Upper Cretaceous of China. – *Cretaceous Research* 32: 495-503.
- Lehman, T.M. & S.T. Wick. 2012. Tyrannosauroid dinosaurs from the Aguja Formation (Upper Cretaceous) of Big Bend National Park, Texas. – *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103: 471-485.
- Loewen, M.A., R.B. Irmis, J.W. Sertich, P.J. Currie & S.D. Sampson. 2013. Tyrant dinosaur evolution tracks the rise and fall of Late Cretaceous oceans. – *PLoS ONE* 8: e79420.
- Longrich, N.R. 2008. A new, large ornithomimid from the Dinosaur Park Formation of Alberta, Canada: Implications for the study of dissociated dinosaur remains. – *Palaeontology* 51: 983-997.
- Lü, J., L. Yi, S.L. Brusatte, L. Yang, H. Li & L. Chen. 2014. A new clade of Asian Late Cretaceous long-snouted tyrannosaurids. – *Nature Communications* 5: 3788.
- McDonald, A.T., D.G. Wolfe & A.C. Dooley. 2018. A new tyrannosaurid (Dinosauria: Theropoda) from the Upper Cretaceous Menefee Formation of New Mexico. – *PeerJ* 6: e5749.
- Osborn, H.F. 1906. *Tyrannosaurus*, Upper Cretaceous carnivorous dinosaur (second communication). – *Bulletin of the American Museum of Natural History* 22: 281-296.
- Persons, W.S. iv., P.J. Currie & G.M. Erickson. 2019. An older and exceptionally large adult specimen of *Tyrannosaurus rex*. – *The Anatomical Record* 2919: 1-17.
- Russell, D.A. 1970. Tyrannosaurs from the Late Cretaceous of Western Canada. – *National Museum of Natural Sciences, Publications in Paleontology* 1: 1-34.
- Sereno, P.C., L. Tan, S.L. Brusatte, H.J. Kriegstein, X. Zhao & K. Cloward. 2009. Tyrannosaurid skeletal design first evolved at small body size. – *Science* 326: 418-422.
- Tsuihiji, T., M. Watabe, K. Tsogtbaatar, T. Tsubamoto, R. Barsbold, S. Suzuki, A.H. Lee, R.C. Ridgely, Y. Kawahara & L.M. Witmer. 2011. Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. – *Journal of Vertebrate Paleontology* 31: 497-517.
- Voris, J.T., D.K. Zelenitsky, F. Therrien & P.J. Currie. 2019. Reassessment of a juvenile *Daspletosaurus* from the Late Cretaceous of Alberta, Canada with implications for the identification of immature tyrannosaurids. – *Scientific Reports* 9: 17801.
- Voris, J.T., F. Therrien, D.K. Zelenitsky & C.M. Brown. 2020 [in press]. A new tyrannosaurine (Theropoda: Tyrannosauridae) from the Campanian Foremost Formation of Alberta, Canada, provides insight into the evolution and biogeography of tyrannosaurids. – *Cretaceous Research* 110: 104388.
- Yun, C.-G. 2016. A review of the basal tyrannosauroids (Saurischia: Theropoda) of the Jurassic Period. – *Volumina Jurassica* 14: 159-164.
- Yun, C.-G. 2017. Testing the hypotheses of the origin of *Tyrannosaurus rex*: Immigrant species, or native species? – *The Journal of Paleontological Sciences* 7: 1-9.
- Yun, C.-G. 2020a. An exceptionally small juvenile *Gorgosaurus libratus* (Dinosauria: Theropoda) specimen from the Dinosaur Park Formation (Campanian) of Alberta. – *The Mosasaur* 11: 107-115.

Yun, C.-G. 2020b. A reassessment of the taxonomic validity of *Dynamoterror dynastes* (Theropoda: Tyrannosauridae). – *Zoodyversity* 54: 259-264.

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