To the editor,

Please find included my review of the manuscript by Washaw et al titled "A transitional species of *Daspletosaurus* Russell, 1970 from the Judith River Formation of eastern Montana". The manuscript has the potential to augment our understanding of *Daspletosaurus* stratigraphy, geography, and potentially tyrannosaurid evolution, however, several key issues will need to be addressed prior to the manuscript being publication ready. Most notably, I have some concerns that the newly proposed holotype may actually represent an individual of *Daspletosaurus torosus* rather than a distinct species. This rationale is based on the specimen being very similar to the few *Daspletosaurus torosus* specimens that are known with many of the proposed autapomorphies of *D. diadematus* even being seen in the *D. torosus* holotype. While I do agree with previous authors (incl. Currie, 2003 and Paulina-Carabajal et al., 2021) that *Daspletosaurus* specimens from the Dinosaur Park Formation (as well as those from stratigraphically equivalent layers within the Oldman Formation south of Dinosaur Provincial Park) are morphologically distinct from those of *Daspletosaurus torosus* from stratigraphically lower deposits of the Oldman Formation within Dinosaur Provincial Park, the newly proposed species is more similar to the latter than the former. I have included photographs below that may assist the authors in their research and would be more than happy to provide additional photos or other materials upon request.

It is important to note, however, that the lack of distinctiveness of '*D. diadematus*' from *D. torosus* does not detract from the scientific importance of the discovery of the proposed holotype BDM 107. The stratigraphic and geographic provenance of the specimen are both critically important data points in the study of tyrannosaurid biology. If the proposed age ranges are accurate (and there are no glaring reasons to suggest they are not), the stratigraphic provenance of the BDM 107 would suggest that *D. torosus* was present during the interval of time for which the Dinosaur Park Formation was being deposited. This could suggest a coeval occurrence of *Daspletosaurus torosus* within Montana and Dinosaur Park Formation *Daspletosaurus* sp. Additionally, this specimen represents the most southeasterly occurrence of *Daspletosaurus torosus* and potentially for all *Daspletosaurus* spp.

For the reasons provided, I propose the manuscript to be in need of **major revisions**. There are some key issues that need to be addressed, however, the study itself is still scientifically significant and therefore is still worthy of publication pending the addressing of these issues. I have included an edited version of the manuscript document which details more specific issues.

Additional Comments

- You'll need to rerun the phylogenetic analysis after addressing the relevant concerns regarding characters and scorings. Be aware, this may alter possible evolutionary scenarios and may therefore need to be addressed in the discussion as well.
- Much of the description is under cited. The authors make several comparisons with other taxa that are not the focus of this study using features that have been previously discussed in the literature. Please add relevant citations to observations/features that are not your own.
- Many parts of the description could benefit from more detail. You have quite a bit of material but tend to be rather brief in your descriptions. For example, you have a very well-preserved postorbital but focus almost entirely the cornual process all while there are plenty of other useful features in this bone including within the ventral ramus and frontal process.

- Grammar and structure could use some work. E.g., many paragraphs are quite short (often being comprised of a single sentence). Try to avoid this where possible. I've marked places where most relevant in the text.

Figure Notes

- Try increasing the brightness on figure 10. As is, its somewhat difficult to see the features you discuss. Also maybe try using a more angled light source to better show off the topography of the bone.
- Some figures could benefit from having additional angles (particularly of structures discussed in the text). For example, an anterior view of the postorbital and ventral view of the squamosal.
- Figure 12 caption states the graphic represents a time calibrated phylogenetic tree however it is not a phylogeny. Please fix.

Comparative Images for the authors

Daspletosaurus torosus holotype CMN 8506 premaxilla in posterior view. Note the foramina in the palatal processes.

D. torosus holotype CMN 8506 right maxilla

CMN 8506 left postorbital in lateral view. Note the subdivision of the cornual process into both the shelf and caudodorsal tuberosity components (also see next picture)

CMN 8506 left postorbital in anterior view also showing separation of the shelf and caudodorsal tuberosity.

CMN 11594 skull roof and left lacrimal+postorbital in lateral view. Specimen comes from the Oldman Fm.

Posteroventral end of cranium of CMN 8506 *Daspletosaurus torosus* holotype. Red arrow indicates quadrate exposure (note surrounding suture lines)

A transitional species of *Daspletosaurus* Russell, 1970 from the Judith River Formation of eastern Montana

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Abstract

The description of a new derived tyrannosaurine, *Daspletosaurus diadematus* sp. nov., provides insight into evolutionary mode in this clade, lending strength to previous hypotheses of anagenesis within *Daspletosaurus* and increasing the resolution with which the evolution of this lineage can be reconstructed. Cladistic phylogenetic methods stratigraphy, and qualitative analysis of the morphology of relevant taxa supports an anagenetic model for the origin of morphological novelty in this taxon, highlighting the predominance of anagenetic evolution among contemporary dinosaur lineages.

Introduction

Since their naming at the turn of the 20th century, tyrannosaurids have captivated public and scientific imagination alike, and are as a result among the best-studied groups of Cretaceous theropods (Osborn, 1905; Brusatte et al., 2010). Perhaps the most successful group of tyrannosaurids were the latest-Cretaceous tyrannosaurines, including among them a diverse array of forms from the slender-snouted alioramins to robust and deep-jawed taxa like *Teratophoneus* and the eponymous *Tyrannosaurus rex* (Lü et al., 2014; Carr and Williamson, 2010; Carr et al., 2011). However, much of the diversity of derived tyrannosaurines remains understudied or poorly understood (Paulina Carabajal et al., 2021), hampering understanding of paleobiogeographic and evolutionary trends (Loewen et al., 2013; Carr et al., 2017; Brusatte and Carr, 2016).

The tyrannosaurine *Daspletosaurus* has been known from Campanian fossil deposits of northern Laurasia for over half a century. However, published work on the phylogeny and paleobiology of this genus is relatively scarce beyond its initial description (Russell, 1970; Paulina Carabajal et al., 2021). Several enigmatic tyrannosaur specimens initially referred to the type species or simply to *Daspletosaurus sp.* (including the recently named *D. horneri*) have been noted as representing novel species by previous workers for several decades (Currie, 2003; Carr, 1999; Carr et al., 2017; Horner et al., 1992; Paulina Carabajal et al., 2021), indicating

Commented [JV1]: +Carr et al., 2017??

Commented [JV2]: I recommend sticking with tyrannosaurid or tyrannosaurine over the more general and less informative moniker of "tyrannosaur" a more speciose genus than has currently been described. Filling this gap is especially pertinent to understanding rates and patterns of speciation in the Campanian of Laurasia, both within tyrannosaurs and among dinosaurs as a whole, as both described species of *Daspletosaurus* have been hypothesized to represent an anagenetic lineage (Carr et al., 2017), including this genus among the many contemporary dinosaur lineages for which anagenesis has been suggested (Horner et al., 1992; Fowler and Freedman Fowler, 2020).

Here we describe *Daspletosaurus diadematus* (sp. nov.). This addition to Campanian tyrannosaurid diversity has the potential to refine existing hypotheses regarding tyrannosaurid evolution in the Late Cretaceous~~,~~ and lends strength to the hypothesis of anagenesis as a predominant mode of evolution in *Daspletosaurus* (Carr et al., 2017).

Tyrannosaurinae Matthew and Brown, 1922 (*sensu* Sereno et al., 2005)

Daspletosaurus Russell, 1970

D. diadematus sp. nov.

Etymology

Diadematus, Latin for “crowned,” in reference to the novel postorbital horn morphology unique to this species, and its diagnosis as a tyrant dinosaur.

Holotype

BDM 107, preserving partial cervical, sacral, and caudal series, a rib, a chevron, a first metatarsal, and a partial disarticulated skull and jaws, including both premaxillae, a right maxilla, jugal, dorsal bar of the lacrimal, quadrate, quadratojugal, and dentary, and a left postorbital and squamosal, and missing the braincase, nasals, palate, and every postdentary bone except for a right splenial. Cranial bones are very finely preserved, with intricate and detailed surface textures especially on the maxilla and postorbital, with teeth preserved in the maxilla, dentary, and one premaxilla. The sacral and caudal centra are preserved in a heavy and hard concretion and are not yet prepared.

Geological Setting

The site “Jack’s B2” was discovered by JW in exposures of the Judith River Formation near Glasgow (Valley County, Montana, USA). This is significantly further east than classic ‘Judith’ localities (Fig. 1), and is sedimentologically atypical, representing distal floodplain and delta sediments deposited during the maximum Campanian regression of the Western Interior Seaway. Here, the Judith River Formation is up to ~48m thick, with the “Jack’s B2” site occurring ~30m below the contact with the overlying Bearpaw Shale.

Precise stratigraphic placement of this easternmost Judith is currently unclear, although an age of ~76.5 Ma seems most likely, which would correlate in time with the lower to middle part of the Dinosaur Park Formation, Alberta (Eberth, 2005; Fowler, 2017). An absolute upper age limit of 75.64 Ma (Ogg & Hinnov, 2012) is delineated by ammonites tentatively identified as *Didymoceras stevensoni* (J. Slattery, pers. comm. 2020) collected by BDM from local outcrops of the overlying Bearpaw Shale (although these were not at the base of the Bearpaw, so older ammonite specimens may be encountered during future prospecting). At present, more precise stratigraphic position can be inferred from the timing of the maximum regression of the Western Interior Seaway during the Campanian (correlated with the R8 regression of Kaufmann, 1977; Rogers et al., 2016). In Alberta and Saskatchewan, the Foremost, Oldman, and Dinosaur Park formations represent early to late subcycles (respectively) of the R8 regression, and of these, the Foremost (~80.5-79.5 Ma) and lower Oldman (~79.5-79.0 Ma; and regional equivalents) are restricted to the west (Alberta and west central Montana)~~,~~ and did not extend as far east as Saskatchewan or our study area in eastern Montana (Eberth, 2005). During late R8, the upper Oldman (~77.5-77.0 Ma) and Dinosaur Park (~76.9-76.0 Ma) Formations were deposited much further to the east, with the lowermost Dinosaur Park recording the R8 maximum regression at ~76.9 - 76.4 Ma (Eberth, 2005; Fowler, 2017). This correlates well with the Judith River Formation of Montana, where Rogers et al. (2016) show the maximum regression of R8 occurring shortly before 76.2 Ma, based on radiometric dates acquired either side of the mid-Judith discontinuity. As such, it seems likely that the study section corresponds in age to the lower to middle part of the Dinosaur Park Formation (although not necessarily lithostratigraphically correlated). A radiometric analysis of a newly discovered volcanic ash is currently underway, and it is hoped that this will provide definitive stratigraphic placement.

Regardless of the precise age of BDM 107, it can be expected to lie intermediate stratigraphically between *D. torosus* (known from the upper Oldman Formation, ~77.0 Ma; Carabajal et al., 2021) and *D. horneri* (known from the Two Medicine Formation, ~75.0 Ma; Carr et al., 2017).

Diagnosis

D. diadematus can be assigned to *Daspletosaurus* based on the following characteristics: extremely coarse subcutaneous surface of the maxilla with no elevated ridges or corresponding fossae; cornual process of the postorbital approaching the laterotemporal fenestra; dorsal postorbital process of the squamosal terminating caudal to the rostral margin of the laterotemporal fenestra; and extremely coarse symphyseal surface of the dentary.

Autapomorphies of *D. diadematus* are as follows: foramen in the dorsal surface of the palatal process of the premaxilla; rounded ventral process of the rostral ramus of the lacrimal; cornual process of the postorbital differentiated into a supraorbital shelf and a caudodorsal tuberosity; very broad, smooth region of bone separating the cornual process of the postorbital from the caudodorsal margin of the orbit; and jugal ramus of the postorbital incised by deep longitudinal (rostrocaudal) sulci.

D. diadematus possesses a unique combination of ancestral and derived *Daspletosaurus* characteristics~~, sharing several of the former with *D. torosus* and the latter with *D. horneri*~~. *D. diadematus* shares with ~~and~~ *D. torosus* ~~share~~ a tall cornual process of the lacrimal (short in *D. horneri*), pneumatic inflation of the lacrimal reaching the medial edge of the bone (this inflation does not reach the medial edge of the bone in *D. horneri*, but see Warshaw, In Review), prefrontal oriented rostromedially (determined from the angle of the prefrontal articular surface on the lacrimal of the holotype of *D. diadematus*, which does not preserve a prefrontal; the prefrontal of *D. horneri* is oriented mediolaterally), pneumatic excavation of the squamosal

Commented [JV3]: This character doesn't appear to be exclusive to *D. diadematus*. The *D. torosus* holotype CMN 8506 also preserves this character (photo included in additional review document)

Commented [JV4]: Also seen in CMN 8506 as well as CMN 11594 (also from low in the Oldman Formation probably close to the same level as CMN 8506)

Commented [JV5]: This also seen in CMN 11594. It's absence in CMN 8506 is probably more so just due to the sheer mass of the boss (no other Daspleto specimen seems to be this way). The center of the boss itself is also pretty far caudal to the orbit

Commented [JV6]: At least from the photos provided, the sulci don't appear to be markedly deeper than those seen in other tyrannosaurids. More clear photos may help to show if the feature truly is unique.

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Commented [JV7]: I have a hunch the lack of inflation on the medial edge of the bone is due to the immaturity/smaller size of the D. horneri specimens. Smaller individuals of Daspletosaurus from the Dinosaur Park Formation also lack this inflation where larger ones possess it. Just a little note!!

Commented [JV8]: You'll need to put the full reference for this in the literature cited

Commented [JV9]: Judging from the frontals of the D. horneri paratype (MOR 1130), it looks as though the morphology would largely be the same as the D. torosus holotype. Can you provide photos showing contrast between all?

that does not undercut its rostromedial margin (entire margin undercut in *D. horneri*), and quadratojugal lacking a pneumatic foramen in its lateral surface (although the presence of this foramen is highly intraspecifically variable in both *D. horneri* and *Tyrannosaurus*, such that further discoveries of *D. diadematus* individuals may reveal its presence in this taxon). *D. horneri* and *D. diadematus* share, to the exclusion of *D. torosus*, a premaxillary tooth row oriented largely mediolaterally, such that all but one premaxillary tooth is concealed in lateral view (rostromedial orientation in *D. torosus* and less derived tyrannosaurids), antorbital fossa of the maxilla terminating at the rostral limit of the external antorbital fenestra (this fossa extends ahead of this boundary onto the subcutaneous surface of the maxilla in *D. torosus* and less derived tyrannosaurids), rostrodorsal ala of the lacrimal inflated (uninflated in *D. torosus* and less derived tyrannosaurids), ventral ramus of the lacrimal longer than the rostral ramus (determined largely by the height of the postorbital bar in the reconstructed skull, given that the ventral ramus is largely unpreserved in the holotype of *D. diadematus*; the rostral ramus of the lacrimal is longer than the ventral ramus in *D. torosus*), and dorsal quadrate contact of the quadratojugal visible in lateral view (concealed in *D. torosus* and less derived tyrannosaurids).

Commented [JV10]: D. torosus holotype is also like this. Carr scores all tyrannosaurids this way too (Carr et al., 2017: character 15)

Commented [JV11]: To be quite honest, I've never fully understood what Carr meant by this feature. At the very least its not a super obvious characteristic. From your photos, D. diadematus seems largely similar to the D. torosus holotype.

Commented [JV12]: Rostrodorsal ala is inflated in CMN 8506. It is scored as inflated for D. torosus by Carr et al., 2017: character 75.

Commented [JV13]: I would be a little cautious here based on how close the structures appear in length from your reconstruction.

Description

Given the wealth of detailed osteologies~~published literature~~ describing tyrannosaurine specimens ~~element-by-element~~ (i.e., Brochu,2003; Hurum and Sabath, 2003; Carr, 1999), our description of the holotype of *D. diadematus* places heavy emphasis on characteristics ~~(or combinations of characteristics)~~ unique to this specimen and those that are otherwise taxonomically or phylogenetically informative within Tyrannosaurinae, so as to avoid the reiteration of plesiomorphic tyrannosaurine morphologies (or synapomorphies of *Daspletosaurus*) already described by previous authors.

Commented [JV14]: Just something to consider, since you are proposing a new phylogeny some of the previous synapomorphies may not be recovered by your tree. You have plenty of space to talk about other characters.

Premaxilla

The premaxillae of *D. diadematus* are similar to those of *D. horneri*, *Tarbosaurus*, and *Tyrannosaurus* in that the alveolar row is oriented largely mediolaterally, such that the rostrum of the skull is broad and the labial surfaces of the premaxillary teeth face rostrally (Fig. 2). In *Tyrannosaurus* and similarly derived tyrannosaurines (*Tarbosaurus* and *D. horneri*), the premaxillary teeth largely overlap each other in lateral view such that only the distalmost tooth is clearly visible; the same would be true of the holotype of *D. diadematus*, were more than a single premaxillary tooth preserved within its socket. Conversely, the premaxillary tooth row of *D. torosus* and less derived tyrannosauroids is oriented rostromedially, such that multiple teeth are clearly visible in lateral view.

Commented [JV15]: See above. All tyrannosaurids have mediolaterally arranged premaxillary alveoli

The body of the premaxilla is subequal in height to the external naris (including the narial fossa and nasal process), as is typical of tyrannosauroids less derived than *Tyrannosaurus* and *Tarbosaurus* (in which the premaxillary body is deeper than the external naris).

Unique to *D. diadematus* among tyrannosauroids is a prominent foramen in the dorsal surface of the palatal process of the premaxilla. The presence of this foramen on both premaxillae suggests that it is not pathological, hence its inclusion here as an autapomorphy of *D. diadematus*.

Commented [JV16]: Also seen in D. torosus and probably even D. horneri (the holotype does have fragments of a premaxilla stored in the type room at the MOR)

There is a small (~2 cm diameter) indentation in the nasal process of the right premaxilla of BDM 107; this is most likely pathological, as it is irregular in form and not present on the left premaxilla.

Maxilla

The maxilla of BDM 107 is irregular relative to other species of *Daspletosaurus* in that it is proportionally elongate, being 64.1 cm in length and 24.8 cm in height (58.6 cm long rostrocaudally and 27.5 cm tall dorsoventrally in *D. horneri*, Carr et al., 2017). Given the broad range of variation in the proportions of this element in other tyrannosaurine species for which larger sample sizes are known (e.g., *Tyrannosaurus*; Paul, Persons, and Van Raalte, 2022; pers. obs., EW), this characteristic was not included as an autapomorphy of *D. diadematus*. Consistency in this trait across further discoveries of *D. diadematus* individuals may require a reevaluation of the taxonomic utility of this character.

As in other *Daspletosaurus*, the subcutaneous surface of the maxilla in *D. diadematus* is densely covered in anastomosing sulci extending from neurovascular foramina (Fig. 3; Carr et al., 2017; Voris et al., 2020). The degree of sculpturing of this surface in BDM 107 is similar to CMN 8506 (*D. torosus*). As in *Thanatotheristes* and other *Daspletosaurus* species, the shallow excavations in between textural ridges that characterize the maxillae of the most derived tyrannosaurines (*Zhuchengtyrannus, Tyrannosaurus*, *Tarbosaurus*) are absent from the holotype maxilla of *D. diadematus*.

D. diadematus possesses~~There are~~ 15 maxillary alveoli, as in other *Daspletosaurus*. XXXX. ~~; t~~ The 13th alveolus bears a swollen abscess in BDM 107, and the 15th maxillary tooth conceals a small replacement tooth within its root that is visible in medial (lingual) view. The first alveolus is ~~not small~~large and bears a typically laterally compressed tooth (i.e., it does not bear a d-shaped crown, similar to that present in the premaxillae).

Jugal

The jugal of *D. diadematus* is most similar to that of *D. torosus* in that it has a mediolaterally thin ventral margin of the orbit (as opposed to a rounded margin as in *Thanatotheristes*; Voris et al., 2022) and does not bow medially along its rostrocaudal length (the jugals of *D. horneri*, *Tyrannosaurus*, and *Tarbosaurus* are angled rostromedially rostral to the orbit, such that the maxillae are medially inset from the orbitotemporal region). No autapomorphies of *D. diadematus* are observable on the jugal (Fig. 4).

Lacrimal

As in all tyrannosaurids except for *D. horneri*, *Tarbosaurus,* and *Tyrannosaurus*, the cornual process of the lacrimal in *D. diadematus* is large~~, pronounced,~~ and ~~comes~~ rises to a distinct apex along its dorsal margin (Fig. 5). This apex is situated directly dorsal to the lacrimal's ventral ramus, as is characteristic of mature tyrannosaurines.

The lacrimal ~~antorbital recess~~sinus differs in morphology from *D. torosus*, but is similar to that of *D. horneri*, *Tarbosaurus*, and *Tyrannosaurus* in that the rostroventral ala joining the

Commented [JV17]: You also have a bowing of the anterior margin of the bone (around the premaxilla-nasal-maxilla contact). It's a little bit more convex than in the holotype of D. torosus. Might be worth mentioning.

Commented [JV18]: Can you show this graphically? If the length/depth ratio plot separated from other Daspleto specimens that would be great for further demonstrating its distinction.

Commented [JV19]: Since these features have been described before you will have to reference them each time. In this case, anastomosing sulci have been noted Daspletosaurus torosus and D. horneri by Carr et al., 2017 and Thanatotheristes by Voris et al., 2020. You'll need to reference those here.

Commented [JV20]: This implies Daspletosaurus has prominent textural ridges where Voris et al., 2020 noted

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Commented [JV21]: You can go more into detail about the teeth themselves. Are they ziphodont or incrassate?

Commented [JV22]: New subject, new sentence.

Commented [JV23]: You have one specimen for D. diadematus therefore you can't say its "typically". If you'r

Commented [JV24]: Is it laterally compressed or is it incrassate as is typical of tyrannosaurids??

Commented [JV25]: Should mention that this is as opposed to Gorgosaurus sensu Currie, 2003 and Voris et a

Commented [JV26]: You could make some more comparisons with other tyrannosaurids. E.g., how does it

Commented [JV27]: This is also the case in D. horneri, Gorgo, Alberto, and Bistahi

Commented [JV28]: This is also the case in Lythonax, usually the case in Tarbo, and sometimes the case in

Commented [JV29]: Ref?

Commented [JV30]: What about the angulation of the posteroventral portion of the lacrimal-jugal contact? In D.

Commented [JV31]: You also have the secondary cornual process mentioned by Carr et al. (2017). Should bring that

Commented [JV32]: The paratype of D. horneri (MOR 1130) has a lacrimal cornual process with a pretty distinct

Commented [JV33]: You've already said large, no need to overstate

Commented [JV34]: Personal opinion: I prefer lacrimal sinus. It's more prevalent in the literature.

Commented [JV35]: In the figure you call it the rostrodorsal ala. Which is it?

rostral and ventral rami of the lacrimal is inflated into a cylindrical bar that is elevated in relief relative to the rest of the recess.

Rostrally, the ventral process of the lacrimal rostral ramus is unique in *D. diadematus* in having a rounded distal end; this process comes to a pronounced tip in all other tyrannosaurids (Carr et al., 2005).

~~Much of the ventral ramus and medial surface of the lacrimal is not preserved in BDM 107, precluding comparison of these regions of the bone.~~

Postorbital

The postorbital is the most conspicuously distinct bone of *D. diadematus*; this element differs from that in all other tyrannosaurids in having a cornual process that is differentiated into two distinct processes: a supraorbital shelf protruding from the dorsal margin of the orbit and a caudodorsal tuberosity emerging more caudoventrally (Fig. 6). These processes are most distinct in caudal or rostral view, where they give the postorbital lateral surface a sinusoidal relief. Both the supraorbital shelf and the caudodorsal tuberosity are situated upon a more ‘typical’ tyrannosaurine cornual process; that is, they lie lateral to a gross swelling of the postorbital similar to that present in other tyrannosaurines. This process is most similar to that of *D. torosus* in that it is hypertrophied to the extent that it overhangs its caudoventral base, forming a crease between the process and the underlying surface of the bone. However, the process’s rostroventral extent is much more broadly separated from the orbit’s caudodorsal margin than in *D. torosus* or any other tyrannosaurid.

Squamosal

~~This element~~The squamosal of ~~is indistinguishable in~~ *D. diadematus* is indistinguishable from *D. torosus* in that:~~.~~ As in the latter, the squamosal of *D. diadematus* has an articular surface for the postorbital that ends caudal to the rostral margin of the laterotemporal fenestra, a pneumatic excavation that does not undercut its rostromedial margin, and a pneumatized caudal process (as evidenced by pneumatic foramina in the process’s rostromedial surface; Fig. 7). The combination of these characters is unique to these two species,~~;~~ however, each one taken individually diagnoses a more inclusive group (*Daspletosaurus*, tyrannosaurines, derived tyrannosaurines, respectively).

Several points of articulation with the rest of the cranium are directly evident on the squamosal, making it important for the reconstruction of the gross morphology of the skull. Rostrodorsolaterally??????, a broad depression receives the caudal ramus of the postorbital, defining the rostral margin of the laterotemporal fenestra. Ventrally, the squamosal articulates with the quadrate and quadratojugal, defining the caudal and lateral boundaries of the adductor chamber. The quadrate, when in articulation with the squamosal and quadratojugal, extends sharply rostromedially, indicating a broad orbitotemporal region, similar to the most derived tyrannosaurines (*D. horneri*, *Tyrannosaurus*, etc.).

Quadratojugal

Commented [JV36]: Avoid one sentence paragraphs. See if you can combine elsewhere.

Commented [JV37]: What about the ventral ramus morphology? How does that compare with other tyrannosaurids and other Daspletos?

Commented [JV38]: See comment in diagnosis

Commented [JV39]: You should include a photo of this angle if its distinct.

Commented [JV40]: If it overhangs only on the posterior side (such that the whole process seems to "curl" posteriorly, the same morphology is also seen in Gorgosaurus, Teratophoneus, and Bistahieversor (we talk about this a little bit in Voris et al., 2022)

Commented [JV41]: I'm not sure I understand what is trying to be said here. Are you saying the Daspletosaurus cornual process sits atop the ancestral tyrannosaurid cornual process or that the cornual process is itsself a secondary ossification or osteoderm that caps the cornual process like what we see in Tyrannosaurus? If the latter say that (see Carr, 2020).

That said, your photos don't seem to show the cornual process as having a capping osteoderm in the same way Tyrannosaurus has them. Can you include a picture?

Commented [JV42]: Vague. Being explicit is generally better.

Commented [JV43]: Grammar and structure here is odd. Try this:

"...: the rostral end of the squamosal-postorbital contact ends caudal to the rostral margin of the laterotemporal fenestra (also in D. horneri), the rostromedial margin of the pneumatic recess on the ventral surface is not undercut, and the caudal process is pneumatized (Carr et al., 2017)."

Commented [JV44]: The lack of undercutting on the rostromedial margin of the squamosal recess is not a tyrannosaurine feature. It was used by Carr et al., 2017 to distinguish D. torosus from D. horneri with D. horneri having the entirety of the recess undercut (see Fig. S2 in the Carr et al., 2017 supplementary information)

Commented [JV45]: Need to reword. Currently, this sentence doesn't really work with the current topic sentence.

Commented [JV46]: Except for the last, all of these features could be more broadly applied to theropods which is irrelevant to the manuscript.

The quadratojugal is conservative morphologically across tyrannosaurids (Loewen et al., 2013). However, two characteristics of the quadratojugal of *D. diadematus* unites it to *D. horneri* and differs from the condition in *D. torosus* and less derived tyrannosaurids. Firstly, *D. diadematus* possesses a dorsal quadrate contact that is broadly visible in lateral view. In most tyrannosauroids, the dorsal quadrate contact of the quadratojugal is directed medially or rostromedially such that it is obscured by the body of the quadratojugal in lateral view. In *D. diadematus* and *D. horneri*, however, this process is directed caudomedially, exposing it laterally (Fig. 8). This characteristic is reversed in the paratype specimen of *D. horneri* (MOR 1130; figure S2K of Carr et al., 2017).~~;~~ ~~Carr et al. (2017) note~~Given that this specimen is younger stratigraphically than the ~~holotype (~~MOR 590~~)~~ (Carr et al., 2017), ~~such that~~ this reversal may ~~represent~~ be~~an~~ ~~anagenetic~~ phylogenetically informative~~signal (~~ or alternatively ~~although~~ may represent intraspecific variation~~ is equally parsimonious in this case)~~. ~~Notably,~~ *Tarbosaurus* and *Tyrannosaurus* also retain the ancestral condition.

Commented [JV47]: Assumption. Could equally as likely indicate cladogenesis in this case. "Phylogenetic" is less presumptive of the underlying patterns.

Commented [JV48]: Parsimonius may imply you have statistically tested this condition. Have you?

Commented [JV49]: Assumption that requires information about your phylogeny first. Just state that Tyrannosaurus and Tarbosaurus share the condition with Daspletosaurus torosus

Secondly, the squamosal ramus of the quadratojugal of *D. diadematus* is broadly separated from the postorbital bar when articulated with the jugal (that is, there is a broad gap between the rostrodorsal extent of the quadratojugal and the rostral margin of the laterotemporal fenestra). The same condition characterizes *D. horneri*, *Tyrannosaurus*, and *Tarbosaurus* to the exclusion of *D. torosus* and less derived tyrannosaurids, in which the squamosal ramus of the quadratojugal nearly contacts the postorbital bar. The separation of the quadratojugal from the rostral margin of the laterotemporal fenestra (and consequent widening of the fenestra) may reflect adaptation towards expanded room for adductor musculature in the orbitotemporal region of the most derived tyrannosaurines, which has been noted by previous authors for *Tyrannosaurus* (Gignac and Erickson, 2017; Carr, 2020).

Commented [JV50]: Note, that there can be quite a bit of variation here and can be very easily skewed by postburial deformation

Commented [JV51]: Also have a look at the supplemental discussion of Brusatte and Carr 2016

Quadrate

No discrete morphological characters distinguish the quadrate of *D. diadematus* from those of its closest relatives. As in other derived tyrannosaurines, the quadrate is massive, with a shallow fossa on its medial surface and a pronounced pneumatic foramen (and surrounding fossa) at the rostral confluence of the mandibular condyles and the orbital process (Fig. 9). The paraquadrate foramen, bounded medially by the quadrate and laterally by the quadratojugal, is small and teardrop shaped; only its lateral margin is made up by the quadratojugal, as the quadrate forms the dorsal and ventral borders of the foramen.

Commented [JV52]: I've really only seen it called the "quadrate foramen" in the literature (though I don't particularly like it because I feel it easily confusable with the quadrate pneumatopore

Although no palatal elements are known, the medial deflection of the quadrate's pterygoid wing allows an approximation of the position of the pterygoids relative to the ~~facial~~ dermatocranium~~skeleton~~, and suggests a broad orbitotemporal region, as in other tyrannosaurines.

Commented [JV53]: Facial doesn't include the squamosal nor quadratojugal bones. Dermatocranial includes all of them

Dentary

The dentary of BDM 107 is deep, with a relatively straight ventral margin and a dorsal (alveolar) margin that trends caudodorsally, increasing the depth of the mandible caudally (Fig. 10). As in other specimens of *Daspletosaurus*, the dentary symphysis is composed of several

Commented [JV54]: You usually describe the feature in "D. diadematus" rather than the specimen number. Either is fine (though I prefer using the specimen over the species names in these instances) but try to be consistent.

interlocking (presumably, as only the left dentary is known) ridges and cusps. There are 17 dental alveoli, as in *D. horneri*, and a sharp, narrow Meckelian groove.

The dentary of BDM 107 has a rugose knob caudoventral to the rostral ~~terminus~~ end of the Meckelian groove; this knob is present in both other species of *Daspletosaurus*, as well as *Tyrannosaurus, Tarbosaurus*, and *Zhuchengtyrannus magnus*, but not *Thanatotheristes* (Carr et al., 2017; Voris et al., 2020).

The lateral surface of the dentary of BDM 107 bears two intersecting grooves caudoventral to the caudal termination of the alveolar margin (Fig. 10); the edges of these grooves are beveled and are likely pathological.

Splenial

The splenial of BDM 107 is typical of *Daspletosaurus* except in the size and form of the mylohyoid foramen (Fig. 11). In most derived tyrannosaurines, including *D. torosus* and *D. horneri*??, this foramen is extremely large, roughly the same dorsoventral depth as the rostral process of the splenial (Carr et al., 2017). In *D. diadematus*, however, the foramen is dorsoventrally ~~narrow~~shallow~~,~~ and rostrocaudally elongate, such that it is ellipsoid in form and roughly half the dorsoventral depth of the ~~splenial's~~ rostral process of the splenial. This is most similar to the condition in alioramins and *Appalachiosaurus*.

Cervical vertebrae

Four cervical vertebrae are preserved in BDM 107 from the cranial-middle portion of the series. No atlas or axis were found. As in all tyrannosaurids, the spinous processes of the cervical vertebrae are subequal in dorsoventral height to their corresponding centra. Both the spinous processes and the centra are craniocaudally short, similar to and most exaggerated in the cervical vertebrae of *T. rex* (see Brochu, 2003, and figures therein). As in *T. rex* (and other large tyrannosaurids), the cranial and caudal faces of the cervical centra are dorsoventrally displaced from one another in order to create the characteristic 'S-curve' of the neck. The centrum of the third cervical vertebra in BDM 107 is extremely foreshortened craniocaudally (i.e., much taller than long), indicating a robustly built cranial portion of the neck, presumably in order to support the weight of the head~~, which is also massive (see above)~~.

Sacral vertebrae

The spinous processes of two sacral vertebrae are preserved. Both are sub-rectangular in form and bear rugose knobs near their apices, presumably the ossified bases of sacral ligaments.

Methods

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The

Commented [JV55]: Are these like those unique to Daspletosaurus in that they are extremely robust peg-and-socket style facets or more like those of other tyrannosaurids in that they are shallower anteroposterior ridges? Could be important to explicitly note

Commented [JV56]: Makes it sound like you're trying to Salt Bae the sentence. Don't be Salt Bae lol

Commented [JV57]: Or other more basal tyrannosaurids(oids)

Commented [JV58]: Can you say anything more about their origin? Are they bitemarks?

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Commented [JV59]: Verify. I don't remember the condition in horneri (or if it even has a splenial preserved)

Commented [JV60]: Avoid using possession.

Commented [JV61]: Rostral process starts at the notch in the dorsal surface. From your photos, it looks like the mylohyoid foramen is the same depth as the rostral process, not half. It is long and shallow though.

Commented [JV62]: You're study is not looking at the condition in alioramins or Appalachiosaurus so unless you've studied them personally you'll need to add references for other studies (e.g., Carr et al., 2005; Brusatte et al., 2012; Foster et al., 2022)

Commented [JV63]: Can you compare and contrast further with other Daspletosaurus and other tyrannosaurid cervicals? D. horneri MOR 1130, D. torosus CMN 8506, D. sp. TMP 2001.36.1 all have cervicals. It would be great if you could to provide some more detail here. Very little has been said of vertebrae morphology in tyrannosaurids.

Commented [JV64]: redundant

Commented [JV65]: Anything else that can be said here?

ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:F7EE2619-89FC-4D72-93DA-EFE6BD549A77. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central SCIE and CLOCKSS.

A cladistic phylogenetic analysis was conducted using the character matrix of Carr et al. (2017) (with modifications from Voris et al., 2020), with additional modifications based on personal observation of specimens made by the lead author, including the addition to the character matrix of several proposed autapomorphies of *D. horneri* noted by Carr et al. (2017) to occur more broadly across Tyrannosauridae (see Supplementary Information for a comprehensive list of modifications). The analysis was run using a "New Technology" search with settings identical to those of Voris et al. (2020) (ratchet, tree drift, tree fusing, and sectorial search set to default, and set to recover minimum length 10 times). Support for recovered clades was tested using bootstrapping with 1000 replicates under a traditional search.

Results

The cladistic analysis produced 12 Most Parsimonious Trees (MPTs; best score: 854). Within the consensus of these trees, the least inclusive clade containing *Dynamoterror* and *Tyrannosaurus* (i.e., all of Tyrannosaurinae more derived than *Alioramus*) was recovered as a large polytomy, with a sister relationship retained between *Tyrannosaurus* and *Tarbosaurus*, and *Dynamoterror*, *Lythronax*, and *Teratophoneus* recovered in a trichotomy.

Given the fragmentary nature of their respective holotypes (scored for <15% of characters), *Nanuqsaurus hoglundi* and *Thanatotheristes* were removed from the dataset, and an additional analysis was conducted as described above. This analysis produced two MPTs (best score: 847), and recovered *D. diadematus* as sister to a clade formed by *D. horneri* and more derived tyrannosaurines (*Zhuchengtyrannus*, *Tarbosaurus*, *Tyrannosaurus*). Alioramins were recovered within a polytomy, as were *Dynamoterror*, *Teratophoneus,* and *Lythronax*; all other topological relationships were as in Voris et al. (2020) (Fig. 12).

Commented [JV66]: Does the inclusion of Thanatotheristes collapse the tree? If not, it could still be a good idea to include (or at the very least to include the second tree in the supplementary data)

Bootstrapping of this result showed weak support (<70) for all clades within Tyrannosaurinae except for alioramini (91), derived tyrannosaurines (*Daspletosaurus* + (*Zhuchengtyrannus* (*Tyrannosaurus* + *Tarbosaurus*))) (80), tyrannosaurines more derived than *Daspletosaurus* (84), and *Tyrannosaurus* + *Tarbosaurus* (72). Recovered support was particularly weak (≤21) for the interrelationships of *Daspletosaurus* (Fig. 12).

An additional autapomorphy of *D. diadematus* was recovered by the cladistic analysis: mylohyoid foramen of the splenial elongate and rostrocaudally ovoid (this foramen is much deeper in other *Daspletosaurus* species).

The *D. diadematus* + more derived tyrannosaurines clade was recovered with the following three synapomorphies: dorsoventrally tall orbit; mediolaterally oriented tooth row of the premaxilla; and squamosal ramus of the quadratojugal broadly separated from the postorbital bar. A further four synapomorphies united *D. horneri* and more derived

Commented [JV67]: Recall from above, however, that D. torosus does have this orientation of the tooth row. You will have to modify some characters as discussed above and rerun your analysis tyrannosaurines to the exclusion of *D. diadematus*: rostrolaterally directed orbits (resulting from the rostromedial bowing of the jugal); cornual process of the postorbital swollen and terminating far rostral to the laterotemporal fenestra; first interdental plate of the maxilla narrow, and second plate truncated (both plates are subsequently expanded in tyrannosaurines more derived than *D. horneri*); and mediolaterally oriented prefrontal.

Additional autapomorphies of relevant taxa and synapomorphies of relevant clades are available in Supplementary Information.

Discussion

Several aspects of the results presented here contrast with (or supplement) those of previous analyses, and therefore deserve mention. Noticeably, the results of the cladistic analysis place *Tyrannosaurus* – line tyrannosaurines (Tyrannosaurus, Tarbosaurus, and Zhuchengtyrannus) ~~within daspletosaurini~~as successive sister taxa to *Daspletosaurus* (*contra* Carr et al., 2017, and Voris et al., 2020, both of which recovered these as sister lineages), and recovers a paraphyletic *Daspletosaurus*; these aspects of the results are the topic of a study by the lead author currently in review, and will not be discussed here. Instead, only the interrelationships and evolutionary history of *Daspletosaurus* are considered below.

Within *Daspletosaurus*, *D. diadematus* fulfills the predictions made by Carr et al.'s (2017) hypothesis of anagenesis between *D. torosus* and *D. horneri.* Namely, *D. diadematus* is stratigraphically, phylogenetically, and morphologically intermediate between these taxa (see Geologic Context, Results, and Diagnosis, respectively), and occurs within the same general geographic range (all three species of *Daspletosaurus* are found within Montana or Alberta; Carr et al., 2017). These points correspond to the criteria proposed by Carr et al., 2017 (and later Zietlow, 2020) for defensible hypotheses of anagenesis: (1) lack of stratigraphic overlap, (2) close phylogenetic relationships, (3) intermediate morphologies, and (4) similar geographic ranges (regarding stratigraphic overlap of *Daspletosaurus* species)~~:~~. ~~note~~ Note that following comments by previous authors, we do not consider Dinosaur Park Formation *Daspletosaurus* material as belonging to *D. torosus* (Currie, 2003; Paulina-Carabajal et al., 2021).~~; s~~Should further analysis demonstrate that it does, or that a *Daspletosaurus* lineage separate from *D. diadematus* exists within the Dinosaur Park formation, the claim of non-overlap will need to be revisited~~; Carabajal et al., 2021; Currie, 2003)~~. We therefore propose that the three species of this genus represent an anagenetically evolving lineage (Fig. 12); this hypothesis will be subject to revision following further study into the phylogenetic affinities of species within the genus, additional discoveries of *Daspletosaurus* individuals from stratigraphically intermediate horizons (which under an anagenetic model, should be intermediate in morphology between species), and characterization of the range of individual variation present in relevant characters proposed here to represent species-level autapomorphies or morphological transitions between taxa.

Should branching events (i.e., cladogenesis) within *Daspletosaurus* be demonstrated by future studies or discoveries, this would not necessarily exclude anagenesis from playing a role in the generation of morphological novelty within the genus. Wagner and Erwin (1995) noted the presence of anagenetic change between branching events in plesiomorphic lineages

Commented [JV68]: You said in the diagnosis that proximity of the cornual process to the laterotemporal fenestra was what united D. diadematus with other Daspletosaurus. How can D. horneri therefore be lacking it?

Commented [JV69]: By definition, Daspletosaurini cannot contain Tyrannosaurus as Tyrannosaurus retains priority

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Commented [JV70]: Important to clarify as the holotype (and many other specimens) of D. torosus are from within the park but from the Oldman Formation not the Dinosaur Park Formation.

Commented [JV71]: There are other abstracts that suggest this too if you want to cite abstracts

Commented [JV72]: New sentence

Commented [JV73]: See my comments in the included document

(=ancestral lineages; the lineage from which cladogenetically derived taxa branch) not in morphological stasis, which led these authors to designate this pattern of speciation as “bifurcation,” reserving “cladogenesis” for branching from morphologically static ancestral taxa. Although we do not adopt their terminology, we agree that anagenesis can operate in concert with cladogenesis in order to produce observed patterns of macroevolutionary change. In the case of *Daspletosaurus*, while autapomorphies of individual species may represent the results of cladogenesis, the synapomorphies of progressively more exclusive clades within the genus (e.g., coarse symphyseal texture of the dentary in *Daspletosaurus*, inflated rostrodorsal ala of the lacrimal in *D. diadematus* + *D. horneri*, etc.) would remain anagenetically derived under a typically cladogenetic model. Anagenesis therefore enjoys a predominant role in the evolution of derived morphologies within derived tyrannosaurines, regardless of the presence of branching events within *Daspletosaurus* (in contrast to morphologically static genera, in which morphological change is concentrated at the base of cladogenetic events; Eldredge and Gould, 1972).

Conclusions

D. diadematus sp. nov., a stratigraphic and morphological intermediate between *D. torosus* and *D. horneri* is hypothesized to represent a transitional form along an anagenetic lineage linking both previously named species of *Daspletosaurus*. This finding, in concert with previous identifications of anagenesis in contemporary dinosaur lineages, emphasizes the explanatory power of anagenesis in the production of evolutionary trends among dinosaurs of the Late Cretaceous Western Interior (Scannella et al., 2014; Freedman Fowler and Horner; Fowler and Freedman Fowler, 2020; Wilson et al., 2020). Indeed, as anagenesis continues to be identified among fossil lineages, the predominant relative frequency of strictly cladogenetic evolutionary models (e.g., punctuated equilibria; Eldredge and Gould, 1972) must eventually come under scrutiny. Future explorations of evolutionary mode in fossil taxa, including further tests of the hypotheses presented here, will be important in this regard, and have the potential to refine understanding of the pattern and process of dinosaur evolution.

Institutional Abbreviations

AMNH – American Museum of Natural History, New York, New York, USA

BDM – Badlands Dinosaur Museum, Dickinson Museum Center, Dickinson, North Dakota, USA

CMN – Canadian Museum of Nature, Ottawa, Ontario, Canada

LACM – Los Angeles County Museum of Natural History, Los Angeles, California, USA

MOR – Museum of the Rockies, Bozeman, Montana, USA

TMP – Royal Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada

UWBM – Burke Museum, Seattle, Washington, USA

ZPAL – Institute of Palaeobiology of the Polish Academy of Sciences, Warsaw, Poland

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Special thanks to Elizabeth Freedman Fowler and Matthew Lavin for discussion and guidance that improved the quality of this manuscript. Thanks also to the members of the field crews that worked tirelessly to excavate “Jack’s B2,” including Steven Clawson, Chalfant Conley, Joshua deOlivera, Jordan Drost, Robert Ebelhar, Elizabeth Flint, Elizabeth Freedman Fowler, Joshua Fry, Felipe Jannarone, Marianna Karagiannis, Ashley Lambert, Rachel Livengood , Kat Maguire, Marcello Toscanini, Alyssa Wiegers, Marianna Rogers, Andrew Chappelle, Emily Waldman, and many others, without whom study of the holotype specimen would not have been possible. Thanks to Steven Clawson, Destiny Wolf, and Darrah Steffen for their preparation of the specimen. This specimen was collected under permit MTM 108829-e6 issued to DF by The US Bureau of Land Management.

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For example, Brusatte and Carr 2016 should be formated like:

Brusatte SL, Carr TD. 2016. The phylogeny and evolutionary history of tyrannosauroid dinosaurs. *Scientific Reports* **6(1):20252** DOI 10.1038/srep20252.

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Supplementary information for: “A new species of *Daspletosaurus* Russell, 1970 from the Judith River Formation of eastern Montana”

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Character Data

Autapomorphies of *Daspletosaurus diadematus*:

Premaxilla

- Foramen in dorsal surface of palatal process

Postorbital

- Cornual process differentiated into a supraorbital shelf and a caudal protuberance
- Cornual process broadly separated from the caudodorsal margin of the orbit by a smooth area
- Jugal ramus incised by deep longitudinal sulci

Lacrimal

- Ventral process of rostral ramus rounded

Additions to character matrix of Carr et al. (2017):

395. **Premaxilla, orientation of alveolar margin: rostromedial-caudolateral, such that several premaxillary teeth are visible in lateral view (0); mediolateral, such that only the distalmost premaxillary tooth is visible in lateral view (1).**
396. **Maxilla, rostral interdental plates, form: first plate truncated, second plate wide (0); first plate narrow, second plate truncated (1); first two plates expanded (2) (Carr et al., 2017)*.**
397. **Lacrimal, orbital margin, form: convex (0); concave (1) (Carr et al., 2017)*.**

Commented [JV1]: See main document. I don't know if this character is accurately representing a phylo signal

398. **Lacrimal, rostroventral edge of rostrodorsal ala, form: sharp, uninflated (0); forming a thick, round bar between rami that is clearly distinct from both the rostral/ventral rami and the remainder of the lacrimal antorbital fossa (1); forming a thick, round bar confluent with rostral and ventral rami but distinct from lacrimal antorbital fossa (2). ORDERED.**
399. **Quadratojugal, dorsal quadrate contact: directed medially, concealed in lateral view (0); directed caudomedially, visible in lateral view (1).**

Commented [JV2]: See review document. This character is seen in D. torosus thus is not phylogenetically informative within Daspletosaurus.

400. **Quadratojugal, squamosal ramus of taxa with constricted laterotemporal fenestrae (*Bistahieversor* + Tyrannosauridae): nearly contacts postorbital ramus of jugal at its rostralmost point (0); well separated from the postorbital ramus of the jugal (1).**

Commented [JV3]: This character implies prior assumptions as to the phylogeny which is kind of a no-no. Also lots of variation here even within species.

401. **Prefrontal, orientation of long axis, dorsal view: rostrocaudal (0); rostromedial or mediolateral (1)(can be scored by the orientation of the prefrontal contact surface on the lacrimal in specimens lacking a preserved prefrontal).**

Commented [JV4]: See manuscript document. I am unable to see much of a difference between the orientation in MOR 1130 from CMN 8506

402. **Squamosal, pneumatic recess, form: not undercut around its entire margin (0); undercut around its entire margin (1) (Carr et al., 2017)*.**
403. **Parietal, joint surface for the squamosal, dorsal extent: covers the ventral half of the base of the caudolateral process (0); covers the entire caudolateral process (1) (Carr et al., 2017)*.**
404. **Prootic, tympanic ridge, presence: does not extend onto the prootic (0); extends onto the prootic (1) (Carr et al., 2017)*.**

*Proposed by Carr et al. (2017) as an autapomorphy of *D. horneri*.

Removed characters (Carr et al., 2017):

28. **Maxilla, maxillary fenestra, caudal margin, shape, lateral view: rounded (0); V-shaped (1) (Brochu, 2003; Loewen et al., 2013:34; Brusatte and Carr, 2016:327).**
The shape of the maxillary fenestra has been demonstrated to be highly variable within *T. rex*; variation in the shape of its caudal margin is taken here to be a result of individual variation (Carr, 2020; Molnar, 1990).
72. **Lacrimal, accessory caudally extending cornual process on the lateral surface between the cornual process and the supraorbital ramus, presence, lateral view: absent (0), present (1) (Carr and Williamson, 2010:70; Brusatte and Carr, 2016:360).**

Commented [JV5]: I don't think this character should be removed. It is a discrete posteriorly directed knob on the lateral surface of the supraorbital ramus. Neither Tarbosaurus nor Teratophoneus have it. It truly does seem to be exclusive to Daspletosaurus. Moreover, it does appear to be present in BDM 107 based on your photos.

We could not identify a discrete difference in the morphology of the caudal end of the rostral ramus of the lacrimal among tyrannosaurines that were scored differently for this character (i.e., *Teratophoneus* and *D. torosus, Tarbosaurus* Fig. 6 Hurum and Sabbath, 2003), and for this reason exclude this character from our analysis.

77. **Lacrimal, transition between antorbital fossa and the subcutaneous surface of the ventral ramus, form, lateral view: surfaces are continuous with each other (0); fossa is deeply inset, forming a ridge along the subcutaneous surface (1) (Carr and Williamson 2010:61; Brusatte et al., 2010:55; Brusatte and Carr, 2016:55).**

Commented [JV6]: Ok to take out

Just a note, this character appears to be ontogenetically acquired within derived tyrannosaurines. Adult and young adult Tyrannosaurus show continuous structures (fused subcutaneous and antorbital) but only the largest Daspletosaurus show evidence of fusion of these structures. Large Albertosaurus, Gorgosaurus, and the Bistahieversor holotype don't seem to be doing this (even those similar in size to Daspleto that do). The question, of course, then becomes how do we determine if a species has it or if we just have a slightly immature individual ¯_(ツ)_/¯

We could not identify a discrete difference in the relief between the antorbital fossa and ventral ramus of the lacrimal in taxa scored for (0) and (1) (i.e., *Bistahieversor* and *D. torosus*) and for this reason exclude this character from our analysis.

134. Quadratojugal, jugal articulation, form, lateral and dorsal views: dorsal quadratojugal process of jugal does not (0) or does (1) approach the base of the quadratojugal (caudoventral corner of the laterotemporal fenestra) (Carr and Williamson, 2010:118; Brusatte et al., 2010:100; Loewen et al., 2013:146; Brusatte and Carr, 2016:100).

We could not identify a discrete difference between the morphology of the dorsal jugal articulation in taxa scored for (1) or (0), and for this reason exclude this character from our analysis.

382. Pes, metatarsal II, lateral surface, shape, proximal view: flat or weakly concave (0); strongly concave (1) (Brusatte et al., 2010:304; Loewen et al., 2013:486; Brusatte and Carr, 2016:304).
This character is redundant with the presence of an arctometatarsalian metatarsus (character 377) and is for this reason excluded from our analysis.

Modified characters (Carr et al., 2017):

69. Lacrimal, cornual process, height, lateral view: tall, greater than 60% height of antorbital fossa below it (0); short, less than 60% of the height of the fossa below it (1) indistinguishable in relief from the rest of the dorsal surface of the lacrimal (2)(var. Loewen et al., 2013:64; Brusatte and Carr, 2016:359). ORDERED.
An additional character state has been added here to distinguish the morphology of the lacrimal's cornual process in *Tyrannosaurus* and *Tarbosaurus* as opposed to more basal tyrannosaurines, including *D. horneri*. Otherwise, we agree with the scorings of Carr et al. (2017), but we note here that the usage of the antorbital fossa as a reference against which to score the height of the cornual process is potentially misleading since the height of the antorbital fossa is itself quite variable between taxa (i.e., CMN 8506, *D. torosus*, vs. MOR 590, *D. horneri*).

110. Postorbital, cornual process, presence and form, lateral view: absent (0); limited to rugose rim at caudodorsal corner of orbit (1); separated from the caudodorsal margin of the orbit and swollen such that the process overhangs its caudoventral margin, forming a crease between the process and the main body of the postorbital (2); entirety of the caudodorsal region of the postorbital inflated, with cornual process expressed as a large, convex boss that grades into the body of the postorbital caudoventrally (3) (Holtz, 2001:56; Sereno et al., 2009:29; Brusatte et al., 2010:81; Loewen et al., 2013:110). ORDERED.
This character is modified to distinguish between the cornual process morphologies of *D. torosus* and *D. horneri* + *Tyrannosaurus*.

Commented [JV7]: This character is problematic and probably oversplitting character states. Need to address below issues.

Commented [JV8]: This is overscoring with Carr et al., 2017: character 112

Commented [JV9]: Note that some tyrannosaurus would score for state 2 including TMP 1981.12.1

160. **Frontal, contribution to orbital rim, dorsal and lateral views: extensive (0), present but limited to a small notch (1), excluded by postorbital-lacrimal contact in large specimens (2), ~~excluded by postorbital-lacrimal articulation and novel palpebral ossification (3)~~ (Sereno et al., 2009:21; Carr and Williamson, 2010:104; Brusatte et al., 2010:120; Loewen et al., 2013:90; Brusatte and Carr, 2016:120). ORDERED.**
State 3 is redundant with character #148 of Carr et al., (2017) (presence of a palpebral ossification), and is for this reason collapsed into state 2.

Modified character states (Carr et al., 2017):

7. ***D. horneri*** **(? → 2)**
Given the relatively complete orbitotemporal region of the holotype of *D. horneri*, we feel comfortable assigning the shape of its orbit to character state 2 (dorsoventrally tall, more than twice as tall as long).

9. ***D. horneri*** **(0 → 1)**
The jugal of *D. horneri* flexes rostromedially at the level of the orbit, directing the orbits forwards as in *T. rex*, such that their orientation is best described by character state 1 (directed rostrally at greater than 20 degrees from the sagittal plane).

23. ***D. horneri*** **(0 → 1)**

Personal observation of the holotype specimen of *D. horneri* (MOR 590) by EW revealed that the maxillary fenestra abuts the ventral margin of the antorbital fossa in this specimen.

38. ***D. horneri*** **(0 → 1)**

Personal observation of the holotype specimen of *D. horneri* (MOR 590) by EW revealed that the antorbital fossa does not extend ahead of the rostral boundary of the external antorbital fenestra in this specimen.

110. ***A. libratus*****,** ***A. sarcophagus*****,** ***Teratophoneus*****, and** ***Qianzhousaurus*** **(2 → 1)**
We regard the morphology of the postorbital's cornual process in the taxa listed above as best represented by character state 1 (i.e., a rugose rim at the orbit's caudodorsal margin) as opposed to 2 (a rugose, convex boss), and sought to distinguish the postorbital morphology of these taxa from the much more prominent cornual processes of derived tyrannosaurines (character states 2 and 3).

Commented [JV10]: Rugose rim indicates the absence of a convex protuberance which all of the ones you removed possess. This state should not be removed.

113. ***D. horneri*** **(1 → 0)**
We disagree with Carr et al.'s (2017) characterization of the postorbital cornual process of *D. horneri* as nearing the laterotemporal fenestra (as is the case in *D. torosus*); we regard the position of this process as more similar to the condition in *T. rex*: widely separated from the laterotemporal fenestra and terminating more closely to the orbit.

Commented [JV11]: However, it does approach in MOR 1130

191. ***D. horneri*** **(1 → 0)**
We disagree with Carr et al.'s (2017) characterization of the suborbital fenestra of *D. horneri* as rostrocaudally elongate; personal observation of the articulated skull of the

holotype specimen of this species (MOR 590) by EW revealed a subcircular fenestra similar to most specimens of *T. rex*.

***Daspletosaurus* autapomorphies recovered by the cladistic analysis:**

D. horneri: 89 (0 → 1), 96 (0 → 1), 158 (1 → 0), 206 (1 → 0), 275 (1 → 0), 305 (2 → 1)

D. torosus: 89 (0 → 1), 272 (0 → 1), 364 (1 → 0)

D. diadematus: 251 (2 → 1)

Synapomorphies recovered by the cladistic analysis:

Daspletosaurus + more derived tyrannosaurines: 20 (0 → 1), 24 (0 → 2), 42 (1 → 2), 43 (0 → 2), 59 (0 → 1), 75 (0 → 1), 76 (1 → 0), 78 (1 → 2), 85 (0 → 1), 87 (0 → 1), 91 (0 → 1), 93 (0 → 1), 97 (0 → 1), 110 (1 → 2), 111 (1 → 2), 117 (0 → 1), 127 (0 → 1), 160 (1 → 2), 220 (0 →1), 231 (0 → 2), 232 (0 → 1), 238 (0 → 1), 361 (1 → 2), 384 (0 → 1)

D. diadematus + more derived tyrannosaurines: 7 (1 → 2), 395 (0 → 1), 400 (0 → 1)

D. horneri + more derived tyrannosaurines: 9 (0 → 1), 110 (2 → 3), 396 (0 → 1), 401 (0 → 1)