A transitional species of *Daspletosaurus* Russell, 1970 from the Judith River Formation of eastern Montana (#75847)

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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 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, 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 characteristics, sharing several of the former with *D. torosus* and the latter with *D. horneri*. *D. diadematus* 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 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).

Description

Given the wealth of 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, so as to avoid the reiteration of plesiomorphic tyrannosaurine morphologies (or synapomorphies of *Daspletosaurus*) already described by previous authors.

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.

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*.

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). 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*.

There are 15 maxillary alveoli, as in other *Daspletosaurus*; 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 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*) 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 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 differs in morphology from *D. torosus*, but is similar to that of *D. horneri*, *Tarbosaurus*, and *Tyrannosaurus* in that the rostroventral ala joining the 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 is indistinguishable in *D. diadematus* from *D. torosus*. 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. Rostrodorsally, 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

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 that this specimen is younger stratigraphically than the holotype (MOR 590), such that this reversal may represent an anagenetic signal (although intraspecific variation is equally parsimonious in this case). Notably, *Tarbosaurus* and *Tyrannosaurus* also retain the ancestral condition.

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).

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.

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 skeleton, and suggests a broad orbitotemporal region, as in other tyrannosaurines.

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 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 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, 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, and rostrocaudally elongate, such that it is ellipsoid in form and roughly half the dorsoventral depth of the splenial's rostral process. 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

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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).

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 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 within daspletosaurini (*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 that following comments by previous authors, we do not consider Dinosaur Park *Daspletosaurus* material as belonging to *D. torosus*; 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 (=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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Figure 1

Map of the area of discovery of BDM 107, holotype of *D. diadematus* sp. nov.

Nearby towns (Hinsdale, Glasgow, Saco) and highways (US-2) are labeled. Dashed lines indicate county boundaries; “Jack’s B2” site indicated by star.

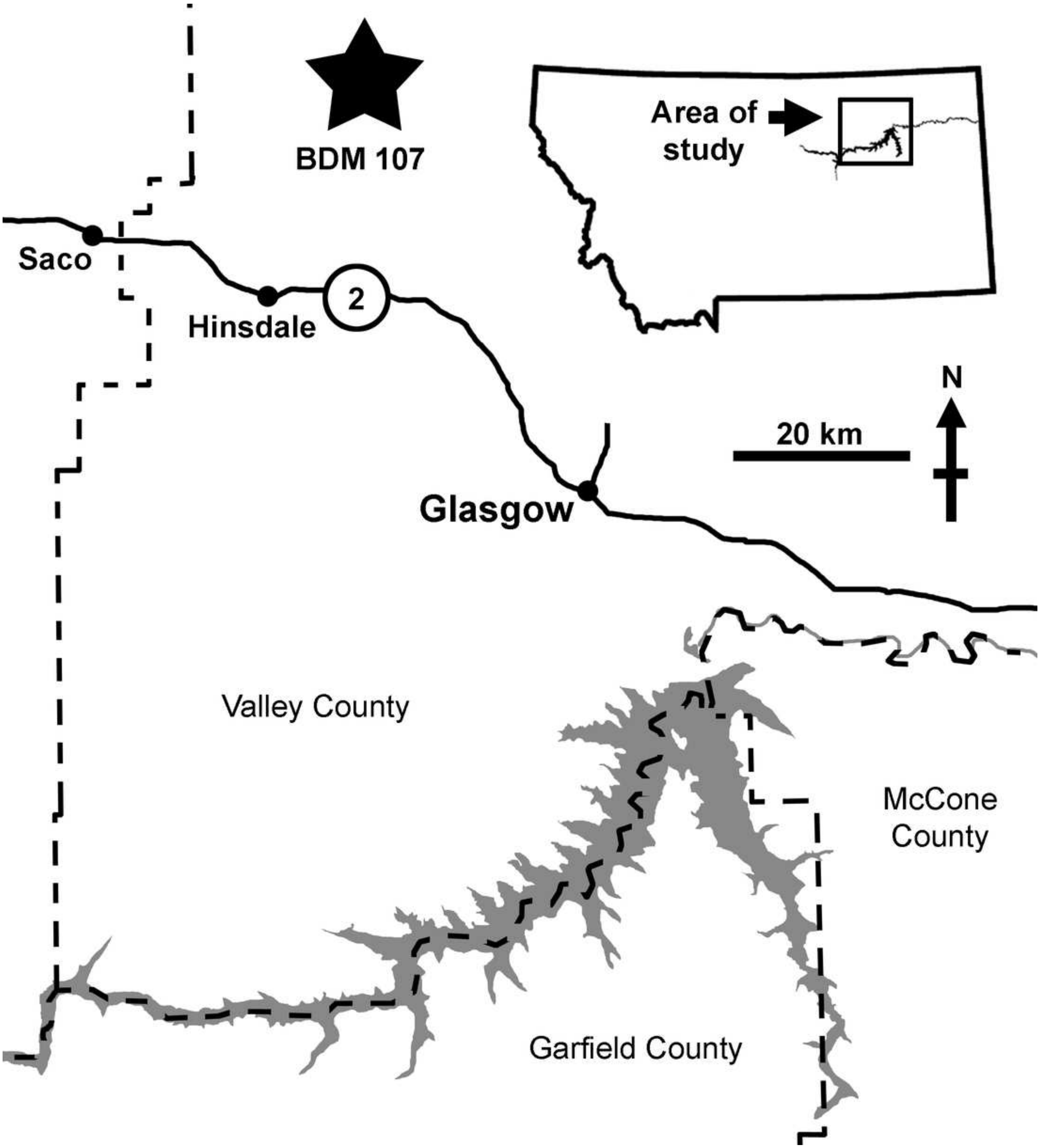

BDM 107
Area of study
Saco
Hinsdale
2
Glasgow
20 km
N
Valley County
McCone County
Garfield County

Figure 2

Premaxillae of BDM 107.

Shown in lateral (A), medial (B), and rostral (C) views. Abbreviations are as follows: nf, neurovascular foramina; psf, palatal surface foramen; smp, symphysis. Scale is 10 cm.

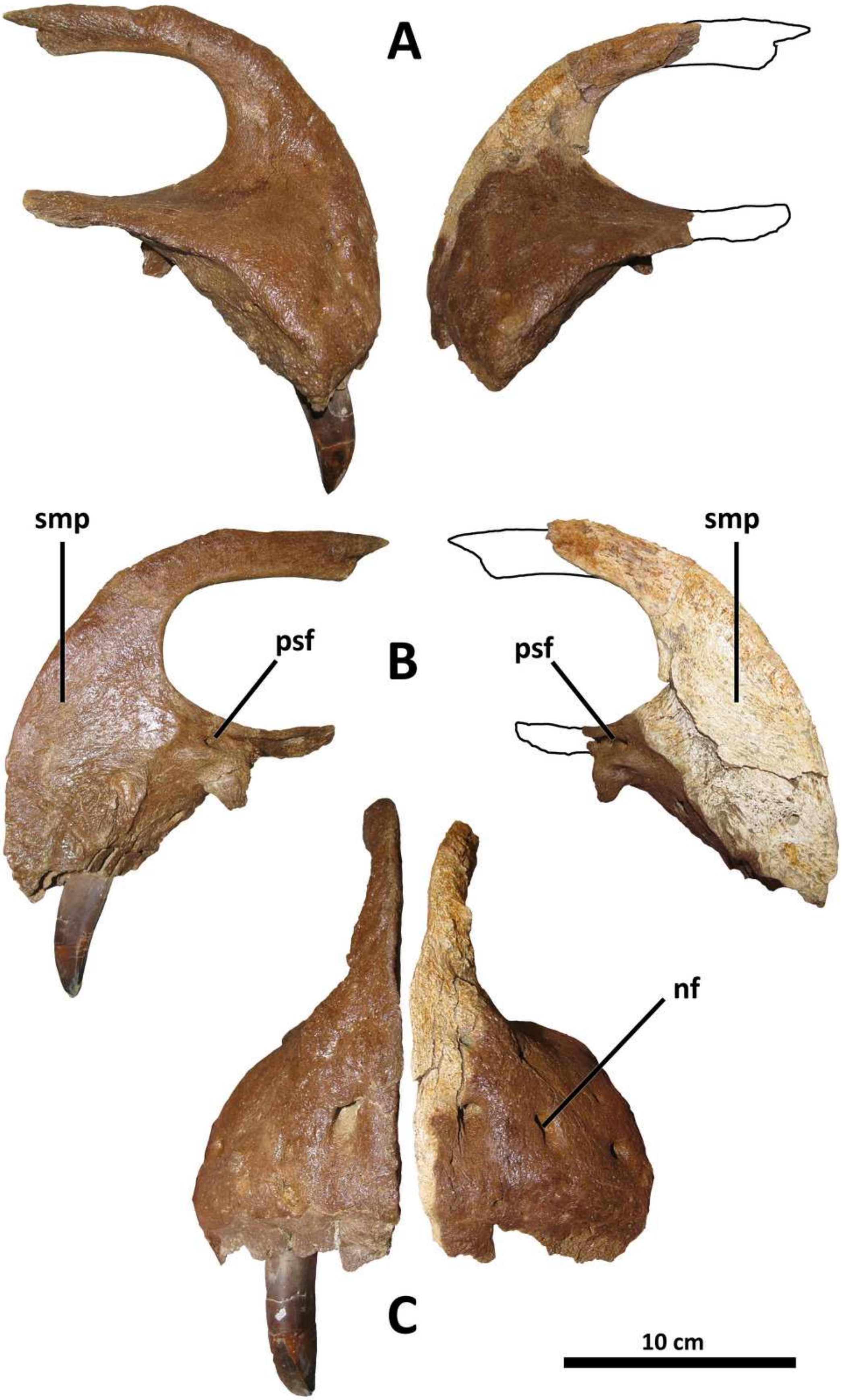

A
B
C
smp
smp
psf
psf
nf
10 cm

Figure 3

Left maxilla of BDM 107.

Shown in lateral (A) and medial (B) views. Abbreviations are as follows: af, antorbital fossa; aof, antorbital fenestra; ma, maxillary antrum; mxf, maxillary fenestra; pmr, promaxillary recess; pmx, promaxillary fenestra; ps, palatal shelf; nf, neurovascular foramina; ns, neurovascular sulci. Scale is 10 cm.

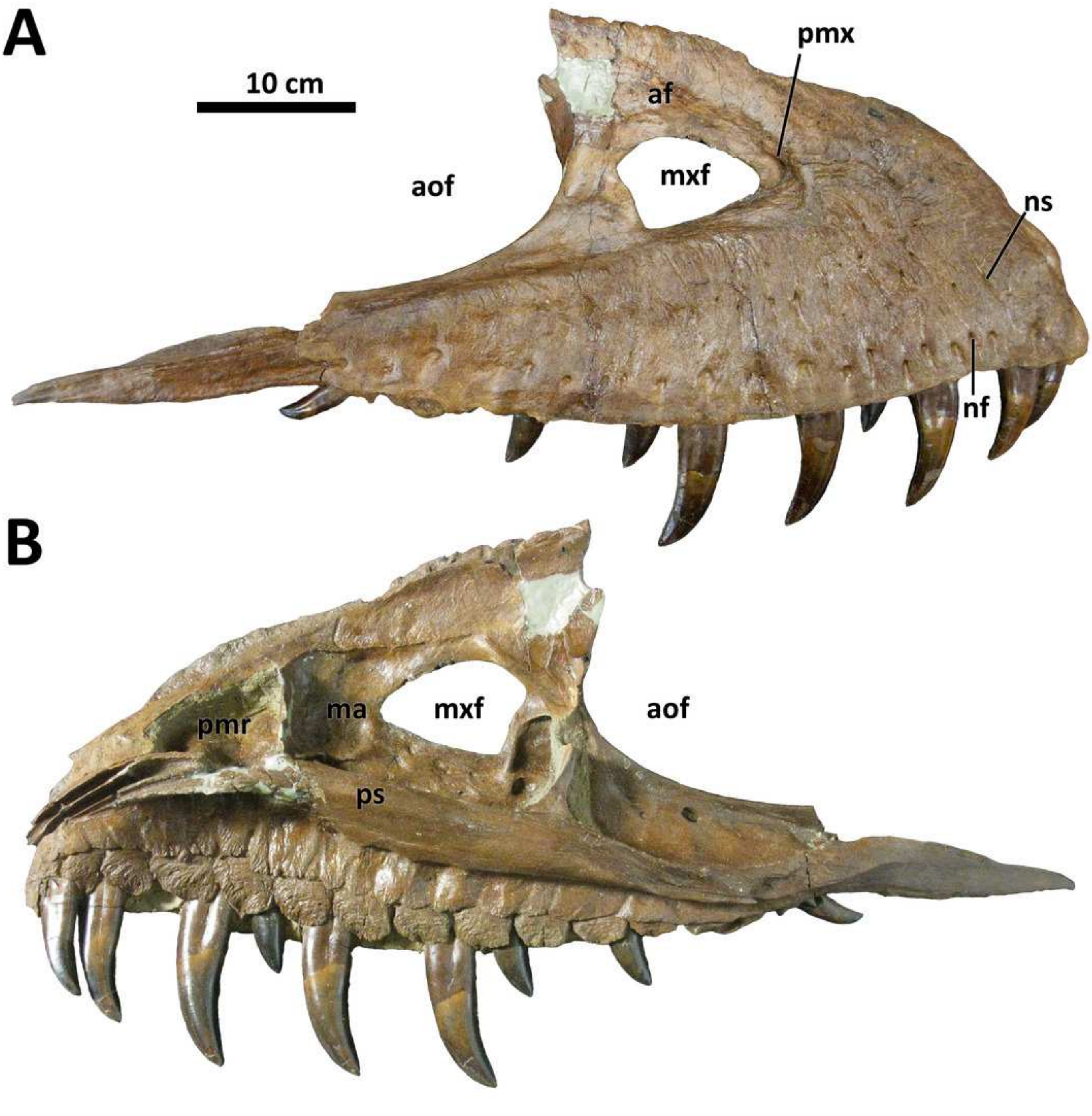

A
10 cm
af
pmx
aof
mxf
ns
nf
B
pmr
ma
mxf
aof
ps

Figure 4

Right jugal of BDM 107.

Shown in medial (A) and lateral (B) views. Abbreviations are as follows: cp, cornual process; po, pneumatic opening; pop, postorbital process. Scale is 10 cm.

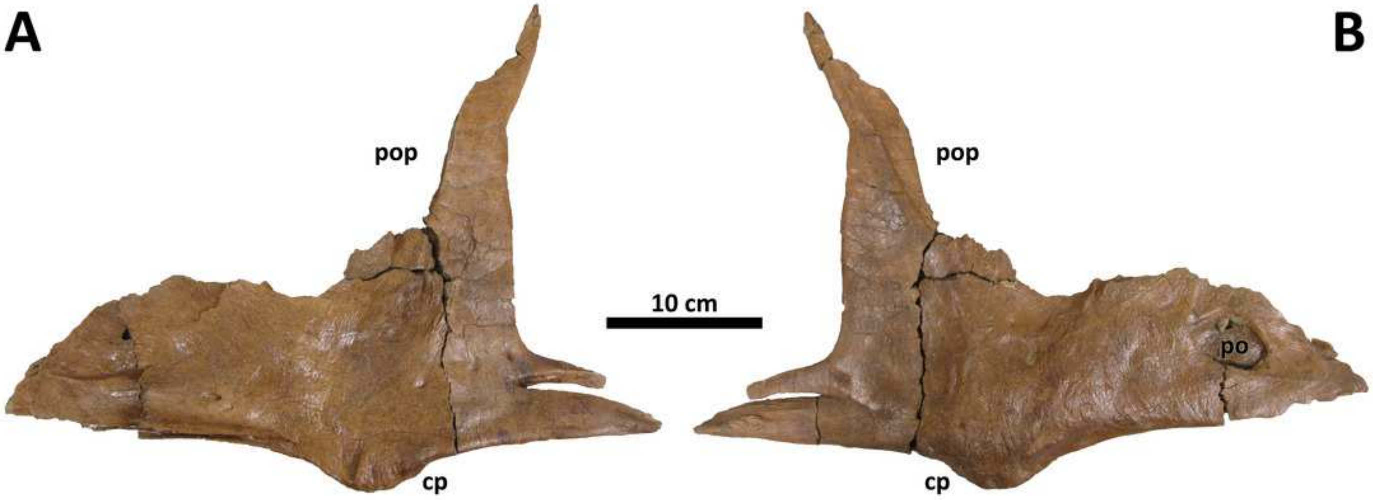


Figure 5

Left lacrimal of BDM 107.

Shown in lateral (A), medial (B), and dorsal (C) views. Abbreviations are as follows: cpa, cornual process apex; fr, frontal ramus; po, pneumatic opening; rda, rostrodorsal ala; rr, rostral ramus; vp, ventral process; vr, ventral ramus. Scale is 10 cm.

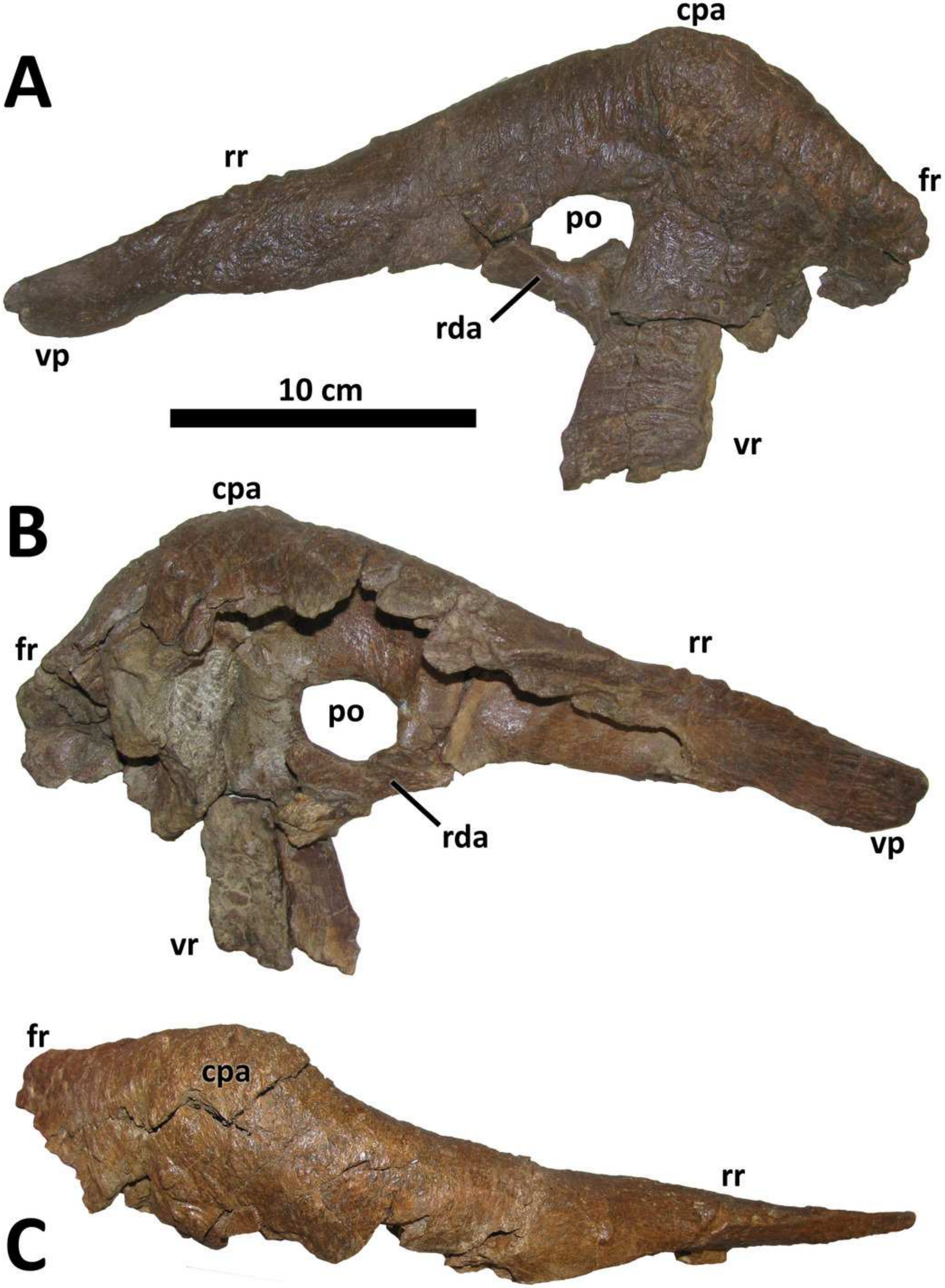

A
cpa
rr
fr
po
rda
vp
10 cm
vr
B
cpa
fr
rr
po
rda
vp
vr
fr
cpa
rr
C

Figure 6

Left postorbital of BDM 107.

Shown in lateral (A) and medial (B) views. Abbreviations are as follows: cdt, caudodorsal tuberosity; fc, frontal contact; lgr, longitudinal ridges; lsc, laterosphenoid contact; sos, supraorbital shelf. Scale is 10 cm.

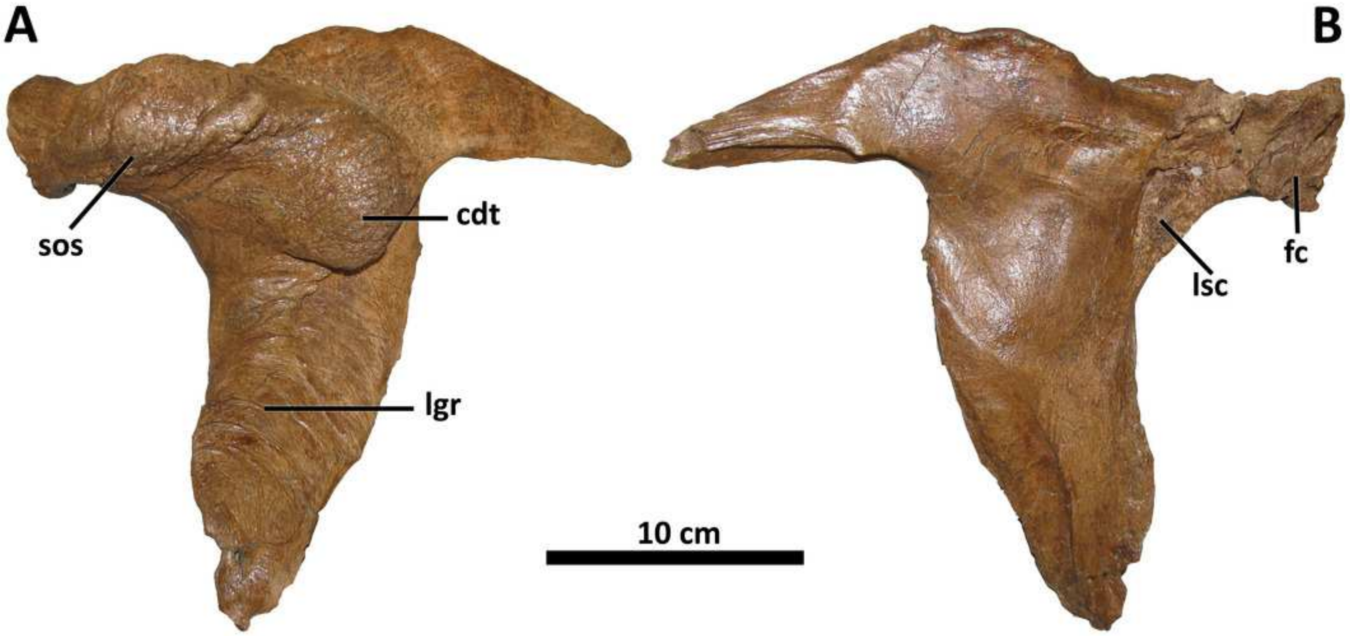


Figure 7

Left squamosal of BDM 107.

Shown in lateral (A) and medial (B) views. Abbreviations are as follows: cp, caudal process; ltf, laterotemporal fenestra; pcs, postorbital contact surface; po, pneumatic opening, qjp, quadratojugal process. Scale is 10 cm.

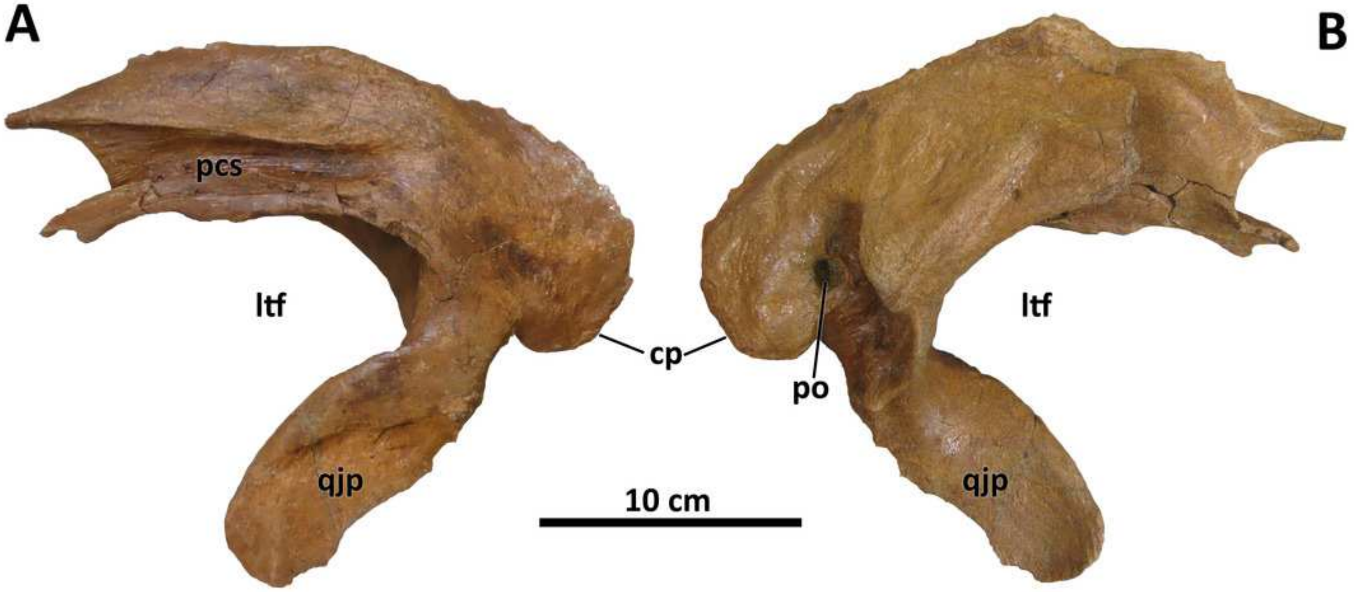


Figure 8

Right quadratojugal of BDM 107.

Shown in lateral (A) and medial (B) views. Abbreviations are as follows: dqc, dorsal quadrate contact; jr, jugal ramus; sc, squamosal contact; vqc, ventral quadrate contact. Scale is 10 cm.

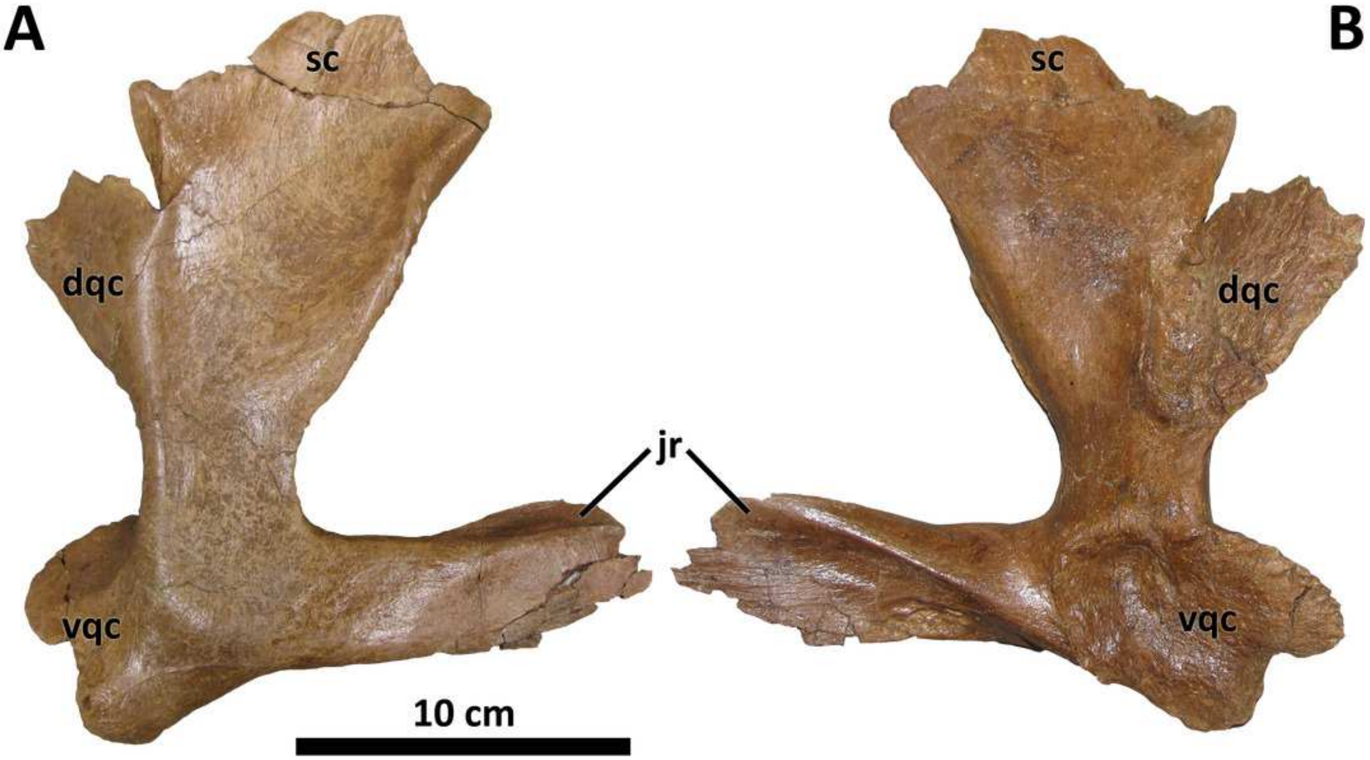


Figure 9

Right quadrate of BDM 107.

Shown in medial (A) and lateral (B) views. Abbreviations are as follows: op, orbital process; mc, mandibular condyles; po, pneumatic opening; pqf, paraquadrate foramen. Scale is 10 cm.

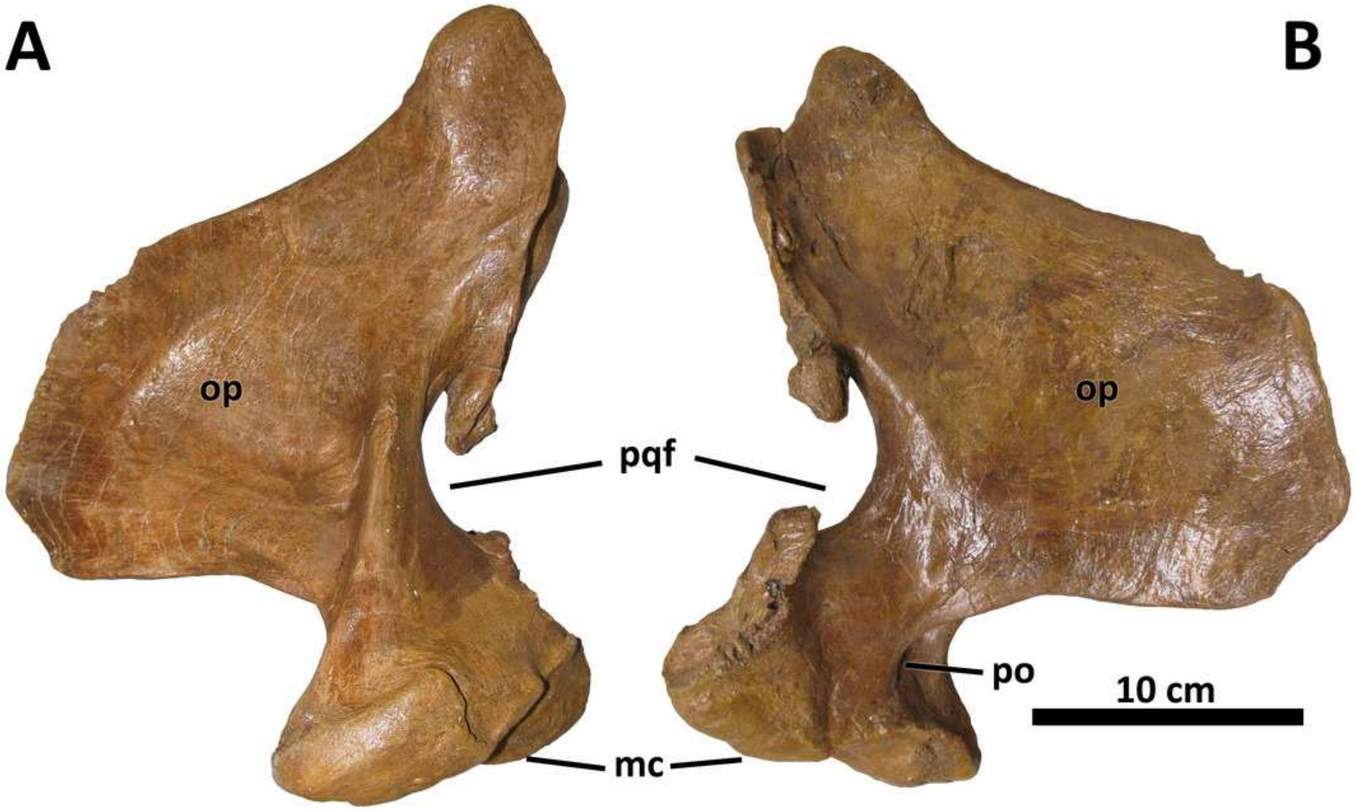


Figure 10

Right dentary of BDM 107.

Shown in lateral (A) and medial (B) views. Abbreviations are as follows: dc, dentary chin; dg, dentary groove; mcf, Meckelian foramen; mg, Meckelian groove; nf, neurovascular foramina; ns, neurovascular sulci; pt, pathology. Scale is 10 cm.

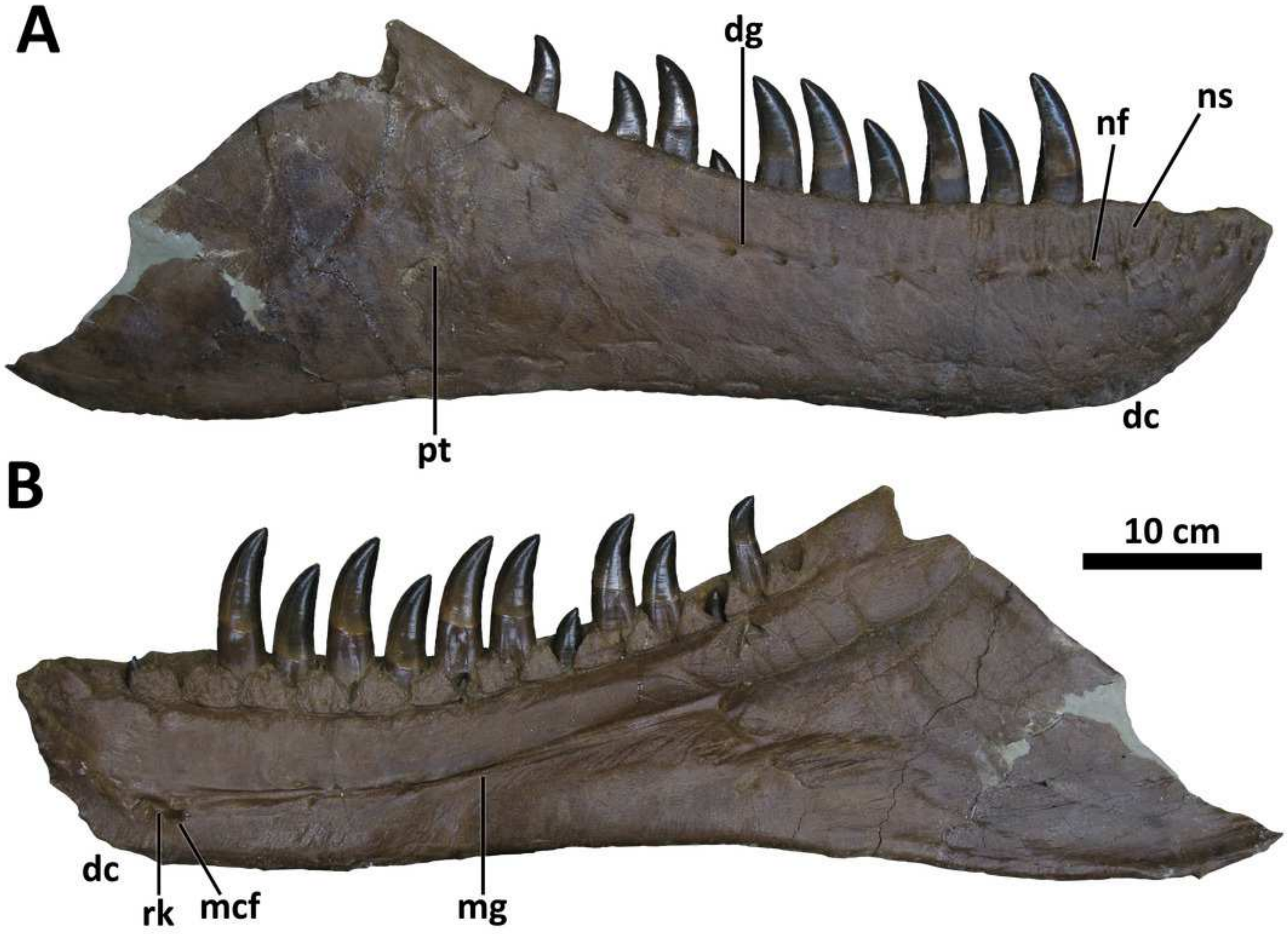


Figure 11

Right splenial of BDM 107.

Shown in medial (A) and lateral (B) views. Abbreviations are as follows: dcs, dentary contact surface; mhf, mylohyoid foramen. Scale is 10 cm.

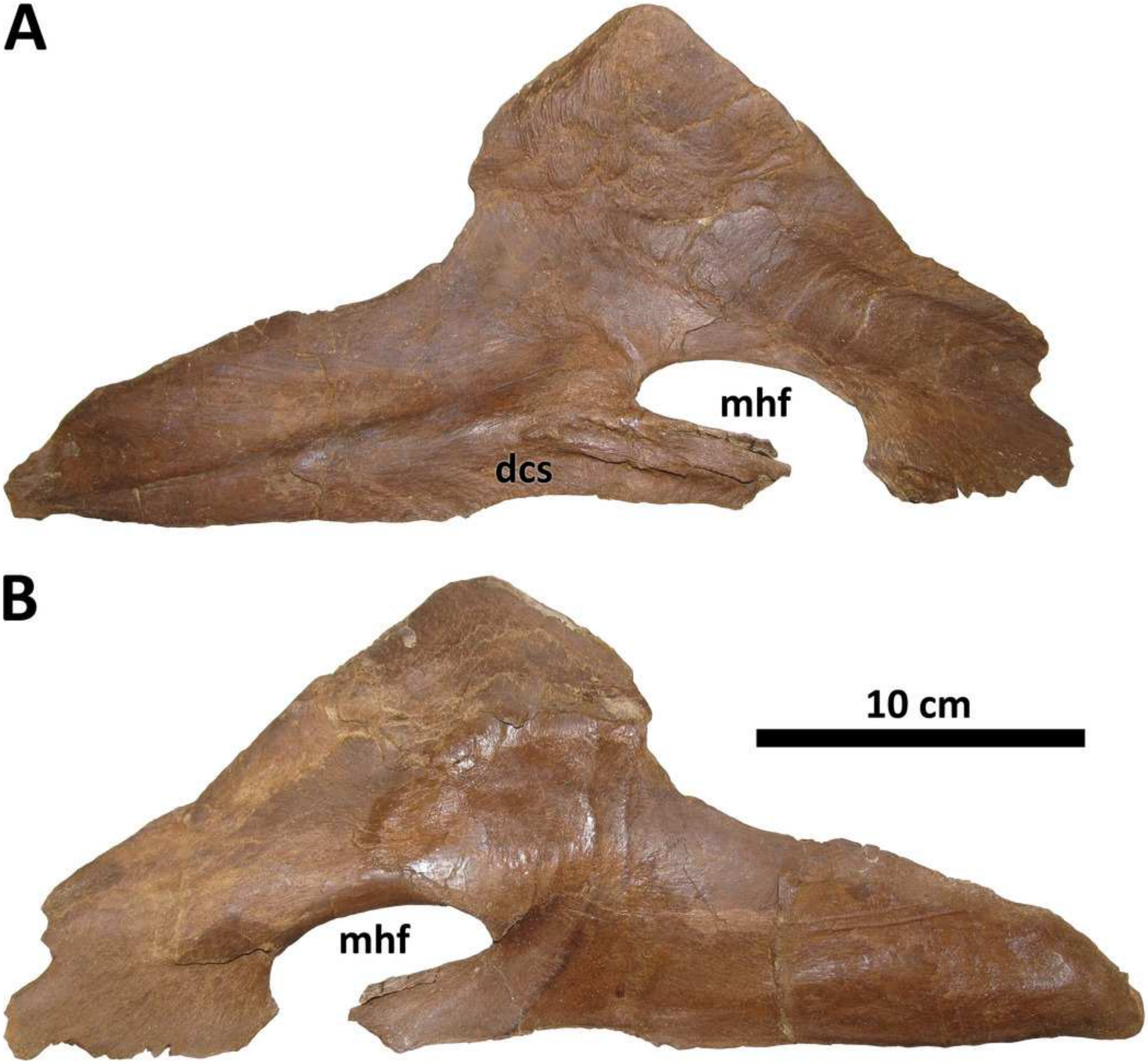


Figure 12

Results of the cladistic analysis.

Grey nodes denote *Daspletosaurus*, star denotes *D. diadematus*, and numbers by each node are bootstrap support. Skull reconstruction represents the holotype of *D. diadematus*, BDM 107.

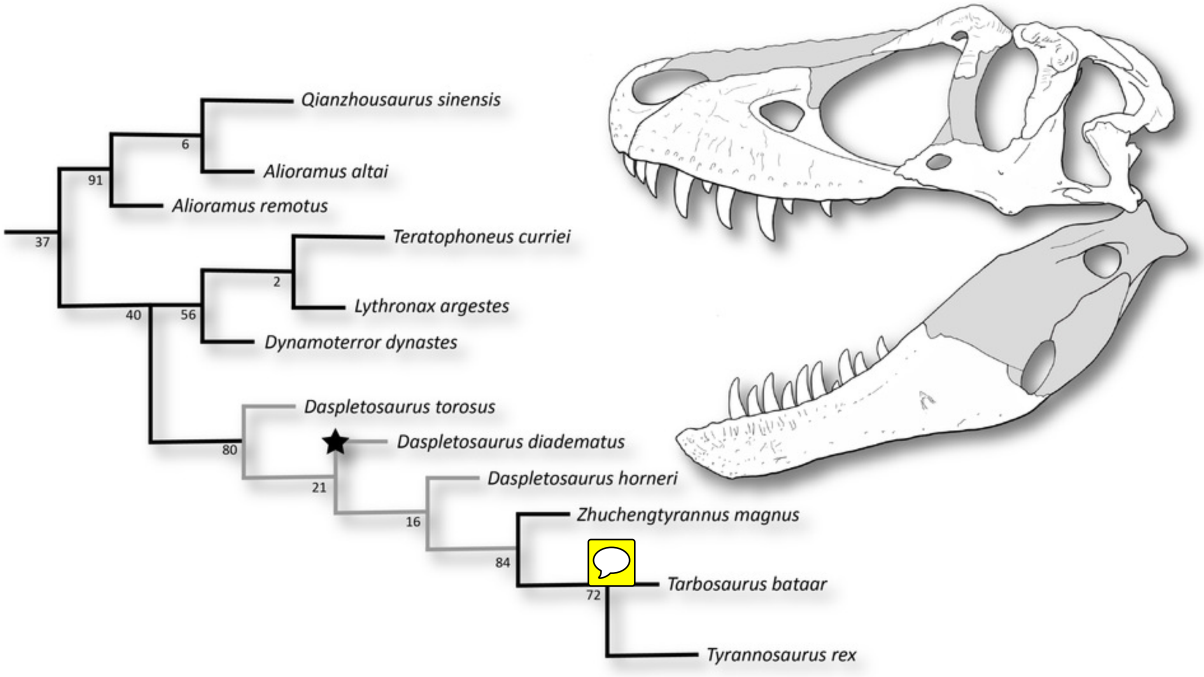
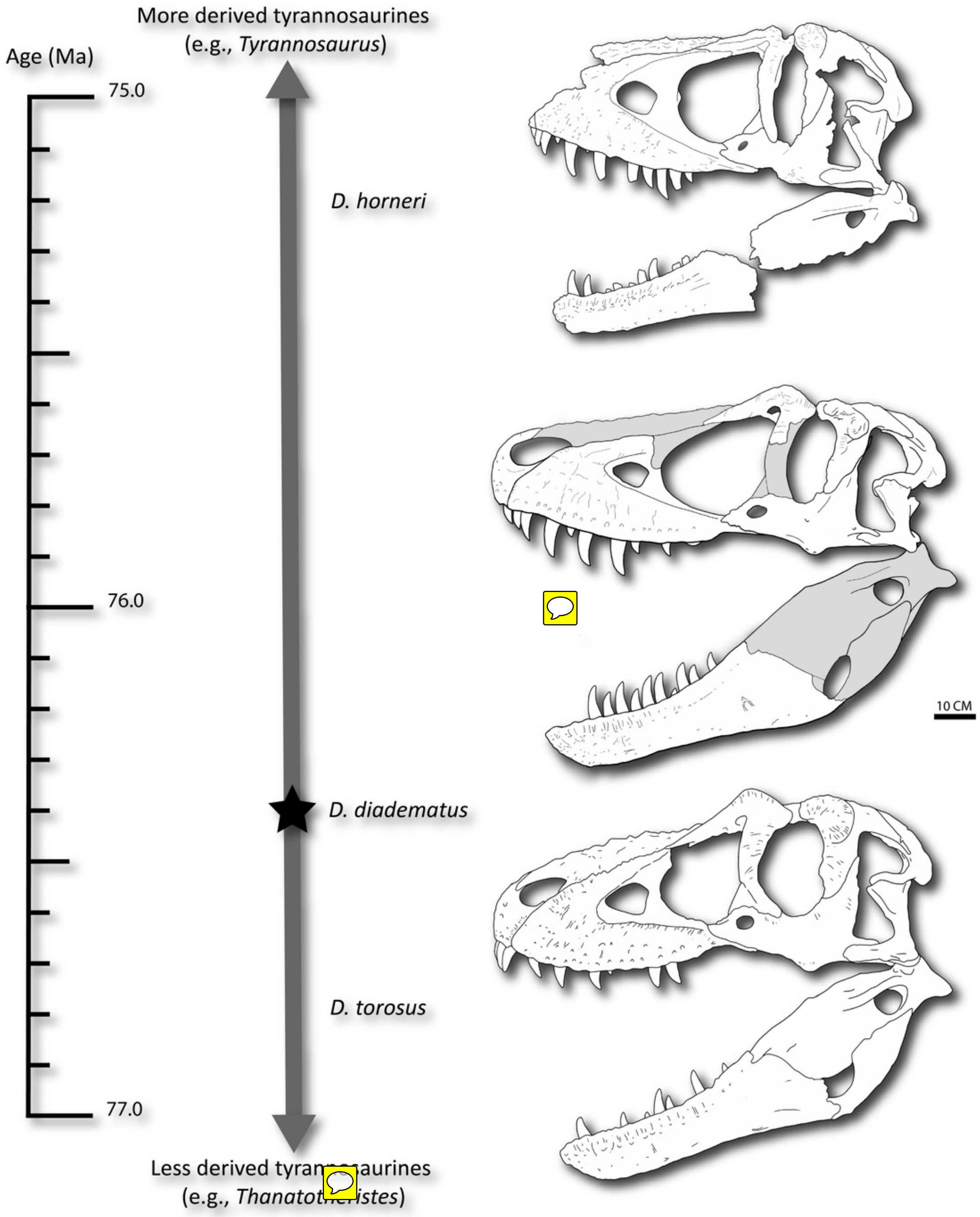


Figure 13

Time-calibrated phylogeny of *Daspletosaur*

Ages (left) are in Ma and are based on Carr et al. (2017) and Fowler (2017) for *D. torosus* and *D. horneri*. Representative skulls are, from top to bottom: *D. horneri*, MOR 590; *D. diadematus*, BDM 107 (known material in white); *D. torosus*, CMN 8506. No clear demarcations are drawn between taxa along the depicted lineage, given the relative paucity of specimens and the subjectivity intrinsic to species delineations of anagenetic lineages. Scale is 10 cm.


More derived tyrannosaurines
(e.g., *Tyrannosaurus*)
Age (Ma)
75.0
76.0
77.0
D. horneri
D. diadematus
D. torosus
10 CM
Less derived tyrannosaurines
(e.g., *Thanatotheristes*)