Behavioral implications of an embedded tyrannosaurid tooth and associated tooth marks on an articulated skull of *Edmontosaurus* from the Hell Creek Formation, Montana

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ABSTRACT

Because teeth can be taxonomically distinct, particularly for non-mammalian carnivores such as non-avian dinosaurs, teeth that have broken off in the bone of another animal during feeding, predation or antagonism can provide direct information on carnivore behaviour. Here, we report on a semi-complete, articulated adult *Edmontosaurus* skull (MOR 1627) from the Hell Creek Formation with an embedded theropod tooth in the nasal. To ascertain taxonomic identity of the preserved tooth tip, we compare standardized crown and denticle measurements as well as denticle descriptions of the embedded tooth to known non-avian theropods recovered from the Hell Creek Formation. We also use computed tomography (CT) scans to investigate the full extent and orientation of the embedded tooth. The apicobasal, labiolingual and mesiodistal dimensions of the tip as well as measured denticle densities and observed denticle characteristics indicate the embedded tooth is from a medium to large bodied tyrannosaurid. The curvature and ovoid cross-sectional shape of the tooth further suggests that the tooth is a maxillary tooth from a middle or posterior tooth position. The lack of reactive bone in the region surrounding the tooth suggests the animal died around the time the tooth became embedded in the nasal. Combined, this information suggests the tooth broke off when a tyrannosaurid bit the snout of the *Edmontosaurus* from the front at or near the time of death of the animal. Comparing observations of hunting and feeding behaviors of modern carnivores specializing in large-bodied prey, the scenario captured by MOR 1627 is most consistent with a bite inflicted during an attempt to control the struggling *Edmontosaurus* or deliver a killing blow followed by carcass consumption.

Subjects Animal Behavior, Ecology, Paleontology
Keywords Tooth marks, Bite marks, Feeding behavior, Paleontology, Paleoecology, Predation, Scavenging

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INTRODUCTION

Tooth marks are produced when one or more teeth contact, and sometimes penetrate, bone. Such marks can provide information on an array of behaviour from carcass consumption

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to intraspecific antagonism (*Erickson & Olson, 1996*; *Jacobsen, 1998*; *Njau & Blumenschine, 2006*; *D'Amore & Blumensehine, 2009*; *D'Amore & Blumenschine, 2012*; *Drumheller et al., 2020*; *Brown et al., 2022a*). Identifying the carnivore(s) responsible for producing tooth marks left behind on bone is often not possible, making behavioural inferences, particularly those surrounding predation and feeding for different taxa, especially difficult. In some rare instances, taxonomic identity can be narrowed down such as when punctures are very deep, exceeding the maximum tooth crown size of most possible carnivores in a formation (*Erickson & Olson, 1996*; *Fowler & Sullivan, 2006*; *Schwimmer, 2010*; *Dalman & Lucas, 2018*; *Peterson & Daus, 2019*), serrated tooth marks, where the spacing of grooves can be approximately correlated to the spacing between denticles and can be used to eliminate possible candidates (*Demere & Cerutti, 1982*; *Schwimmer, Stewart & Williams, 1997*; *D'Amore & Blumenschine, 2012*), and embedded teeth, where a part of a carnivore's tooth breaks off and becomes lodged in the animal being fed and/or preyed upon (*Currie & Jacobsen, 1995*; *Chin, 1997*; *Schwimmer, Stewart & Williams, 1997*; *Everhart, 2008*; *Ehret, MacFadden & Salas-Gismondi, 2009*; *Bell & Currie, 2010*; *Xing et al., 2012*; *Perez, Godfrey & Chapman, 2021*). Embedded teeth are perhaps the best way to identify the producer of a tooth mark as teeth are taxonomically informative, at least to the family level, and in some cases, to the species level (*Currie, Rigby Jr & Sloan, 1990*; *Peng, Russell & Brinkman, 2001*; *Sankey et al., 2002*; *Smith, Vann & Dodson, 2005*; *Samman et al., 2005*; *Larson, 2008*; *Evans, Larson & Currie, 2013*). The positioning of the embedded tooth can also provide information on orientation of the bite, allowing for more detailed descriptions of behaviour. Here, we present on an *Edmontosaurus* skull from the Maastrichtian Hell Creek Formation with an embedded theropod tooth crown and associated tooth marks which preserves potential evidence of predator–prey interactions.

MATERIALS AND METHODS

Background

The Hell Creek Formation primarily consists of interbedded fluvial sandstones and mudstones and records the end of the Mesozoic Era in Montana and surrounding regions (*e.g.*, *Clemens & Hartman, 2014*; *Hartman et al., 2014*; *Fowler, 2020*). Non-avian dinosaurs preserved in the formation include well-known taxa such as *Tyrannosaurus, Triceratops,* and *Edmontosaurus* (*e.g.*, *Brochu, 2003*; *Horner & Goodwin, 2006*; *Campione & Evans, 2011*). Large sample sizes available for these terminal Cretaceous taxa provide insights into their ontogeny and evolution (*e.g.*, *Horner & Goodwin, 2006*; *Campione & Evans, 2011*; *Scannella et al., 2014*; *Carr, 2020*; *Woodward et al., 2020*; *Wosik & Evans, 2022*) and contribute to hypotheses regarding their behaviour (*e.g.*, *Farke, Wolff & Tanke, 2009*; *Mathews et al., 2009*; *Longrich et al., 2010*; *Horner, Goodwin & Myhrvold, 2011*; *Peterson & Daus, 2019*).

In 2005, Museum of the Rockies (MOR) specimen 1627 was discovered by Marge Baisch and collected by Ken Olson in the Hell Creek Formation of Dawson County, Montana (MOR locality no. HC-387). MOR 1627 is a nearly complete, articulated *Edmontosaurus* skull that was discovered in a sandstone unit of the formation on lands managed by the

Bureau of Land Management. Precise stratigraphic placement of the locality within the formation remains to be determined. The specimen was prepared by Carrie Ancell at MOR.

Tooth mark description

Tooth marks can be described using an ichnological or taphonomic framework (*Zonneveld et al., 2022*). Recently, *Zonneveld et al. (2022)* advocated for the use of terminologies that are well-established and accessible to the broader scientific community. Following these recommendations, we have chosen to utilize the recently proposed Category-Modifier system as it synthesizes, refines and expands upon previous taphonomic terminologies historically used to describe dinosaurian tooth marks (*e.g.*, *Erickson & Olson, 1996*; *Fowler & Sullivan, 2006*; *Hone & Watabe, 2010*; *Hone, Tanke & Brown, 2018*; *Brown, Tanke & Hone, 2021*).

To obtain the full dimensions of the embedded tooth, MOR 1627 was CT-scanned at Advanced Medical Imaging at Deaconess Hospital in Bozeman, Montana, using a Toshiba Aquilion CT Scanner. 3D models were constructed using these scans with 3D Slicer and exported to Blender for measurement of the apicobasal (~crown base height, CBH), mesiodistal (~crown base length, CBL) and labiolingual (~crown base width, CBW) dimensions of the preserved tooth. Measurements of the embedded tooth and tooth marks are available in Tables S1–S2.

RESULTS

MOR 1627 is a partial, adult *Edmontosaurus annectens* skull from the Maastrichtian Hell Creek Formation of Montana with an embedded non-avian theropod tooth tip. Elements on both sides of the skull are preserved in articulation and relatively complete except for the region anterior to the right maxilla which is mostly missing. The surangular and angular are also missing on the right side of the skull. The left dentary lacks a symphyseal process and the portion of the dentary ramus anterior the tooth row has been broken such that the broken edges of the bone anterior the break rest on top of the portion of the ramus posterior the break. The tooth penetrates the dorsal surface of the left nasal and protrudes down into the external nares (Fig. 1) with the labial or lingual surface of the tooth visible in the left lateral view of the skull. Part of the tooth is visible in dorsal view and accompanied by four possible tooth marks located on the dorsal surface of the left nasal (Fig. 1).

In addition to the embedded tooth, a total of 23 possible tooth marks were identified on the skull—nine on the left and 14 on the right. The four possible tooth marks on the left nasal, as defined under the Category-Modifier system of *Wyenberg-Henzler et al. (2024)*, consist of two curved scores (marks 2 and 4) and two pits (marks 3 and 5) (Table S1) (Fig. 1). Four tooth marks, consisting of one linear furrow (mark 6), two linear scores (marks 7 and 9) and a curved score (mark 8), are located on the left jugal below the orbit. Two curved scores (marks 10 and 15), four linear scores (marks 11, 13, 16 and 17) and two pits (marks 12 and 14) are observed on the right mandible on the coronoid process. The remaining six marks are located on the ramus of the right dentary—five curved scores (marks 18, 19, 21, 22, 23) and one linear score (mark 20). Most of the marks observed on MOR 1627 are smooth-edged except for one mark on the right coronoid process (mark

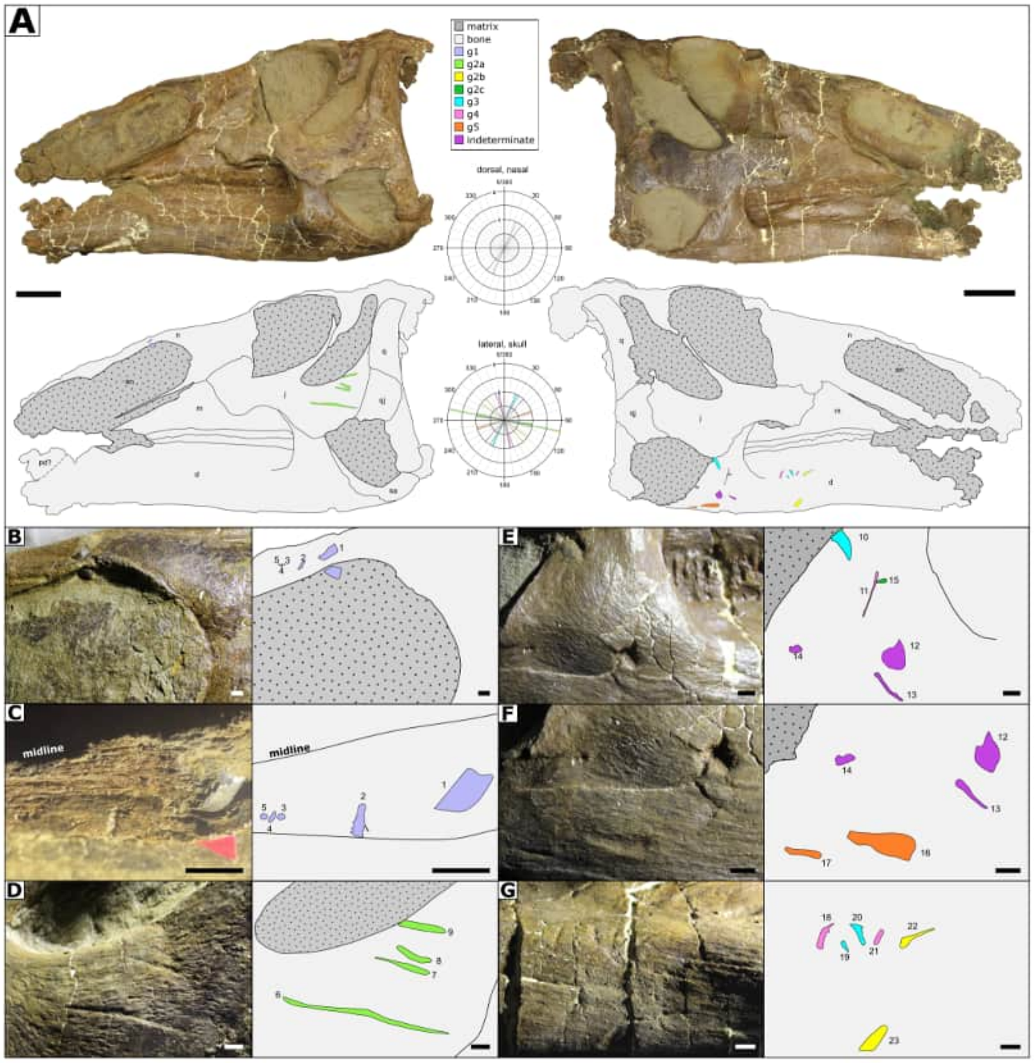

Figure 1 Skull of MOR 1627 showing location and orientation of the embedded tooth and associated tooth marks. (A) Skull in lateral view with corresponding line drawings. Top rose diagram shows the orientation of tooth marks on the dorsal surface of the left nasal with the anteroposterior axis along 90°/270°. Bottom rose diagram shows the orientation of the remaining tooth marks standardized to the left lateral view of the skull with the anteroposterior axis at 0°/180° and anteroposterior axis at 90°/270°. (B) Embedded tooth and associated tooth marks on left nasal in lateral view. (C) Embedded tooth and associated tooth marks on left nasal in dorsal view. (D) tooth marks on left jugal in lateral view. (E) Tooth marks on base of right coronoid process in lateral view. (F) Tooth marks on right dentary and base of right coronoid process in lateral view. (G) Tooth marks on right dentary along mandibular ramus in lateral view. Scale bars are 10 cm in (A) and one cm in (B–G).

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14) and one on the mandibular ramus of the right dentary (mark 18) which are both rough-edged. All marks are also internally smooth with the exception of mark 6 on the left jugal which shows a spongey texture anteriorly and becomes smooth posteriorly. A total of seven tooth mark groups were identified based on similarities in location and orientation, with three marks that could not be assigned to a group (Table 1).

Table 1 List of tooth mark groups with locations and orientations for MOR 1627. Orientation of group 1 marks is relative to the anteroposterior axis (90°/270°) of the left nasal. All other orientations are relative to the anteroposterior axis of the skull in left, lateral view with dorsoventral at 0°/180° and anteroposterior axis at 90°/270° .

Location	Group	Mark #	Orientation range (°)
Middle of left nasal, dorsal surface	1	1, 2, 3, 4, 5	25–38
Left jugal below the orbit, lateral surface	2a	6, 7, 8, 9	98–105
Right mandible, lateral surface	2b	22, 23	126–140
	2c	15	102
	3	10, 19, 20	25–31
	4	11, 18, 21	162–169
	5	16, 17	72–75
	indeterminate	12, 13, 14	43

The tip of the tooth is directed ventrally, curving slightly towards the anterior end of the skull. Thus, the mesial surface of the tooth is closest to the posterior end of the skull and the distal surface of the tooth is closest to the anterior end of the skull (Figs. 1 and 2). Mesial denticles are preserved and visible in left lateral view and some of the apical-most distal denticles are visible in oblique, lateral view but most are obscured by matrix. Mesial and distal denticles are roughly equal in size and proximodistally sub-rectangular in shape. The apical and basal edges of the denticles on both carinae are rounded (*i.e.,* have a relatively symmetrical margin), do not show any obvious curvature apically and are oriented approximately perpendicular to the apicobasal axis of the tooth. There are no visible blood grooves on the tooth. Denticles have an apicobasal height of 0.43–0.5 mm and mesiodistal length of 0.38–0.58 mm with approximately 1.76 denticles per mm along the mesial carinae and 1.28 denticles per mm along the more apical region of the distal carinae (Table S2). Macrowear is visible on the tip of the tooth as the first couple apical denticles have been removed and the region with the missing denticles are smooth. Fine mesiobasal-apicodistally oriented microstriae (*i.e.,* microwear) are also visible on the labial/lingual surface of the tooth. CT data indicates that the tooth penetrates the left nasal at an oblique angle (Fig. 2). The tooth is ovoid in cross section with a preserved crown base length of approximately 19.9 mm, crown base width of 12.3 mm and crown height of 22.0 mm (Table S2).

DISCUSSION

Taxonomic identification

The embedded tooth of MOR 1627 is most likely from a non-avian theropod given the presence of denticles (eliminating crocodylians and pterosaurs) and the preserved crown height exceeds that of lizards and avians recovered from the Hell Creek Formation. Various tooth-bearing non-avian theropods have been recovered from the Hell Creek Formation: *Acheroraptor temertyorum*, cf. *Saurornitholestes langstoni*, *Richardoestesia isosceles*, *Troodon*

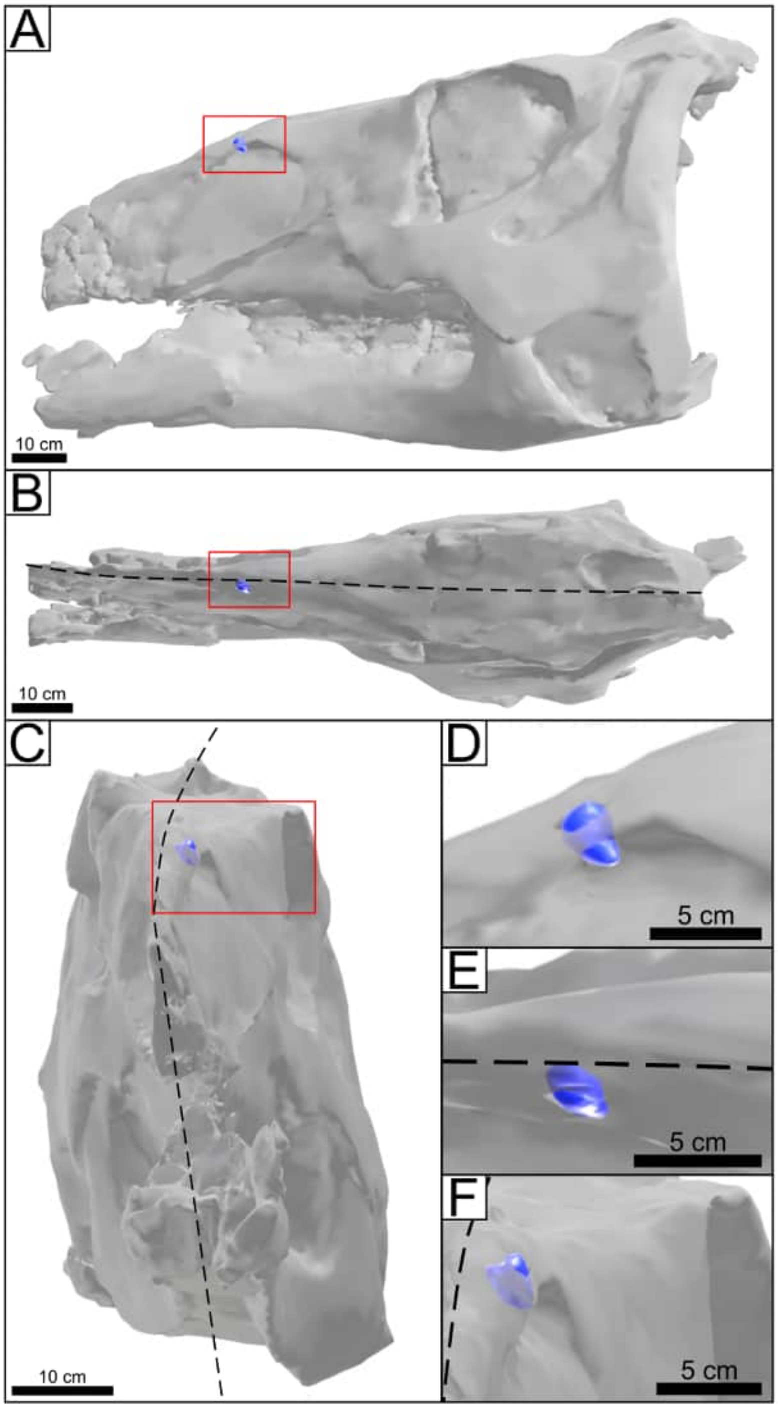

Figure 2 **Three-dimensional model rendering from CT data for MOR 1627.** (A) Left lateral view of entire skull with close-up (D) of the embedded tooth. (B) Dorsal view of entire skull with close-up (E) of the embedded tooth. (C) Anterior view of entire skull with close-up (F) of the embedded tooth. Dashed lines indicate the specimen midline.

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sp. *Paronychodon lacustris*, *Dakotaraptor steini* and *Tyrannosaurus rex* (*Brown, Currie & Therrien, 2022b*). Recent studies have suggested the presence of multiple species of *Tyrannosaurus* in the latest Maastrichtian (*Paul, Persons & VanRaalte, 2022*; *Paul , 2025*), a hypothesis disputed by other theropod workers (*Carr et al., 2022*; *Carr, 2025*). Further, debate has surrounded the taxonomic status of smaller-bodied tyrannosaur specimens from the Hell Creek Formation, which have been hypothesized to represent a distinct taxon, *Nanotyrannus lancensis* (*e.g.*, *Bakker, Michael & Currie, 1988*; *Longrich & Saitta, 2024*, but see *Carr, 1999*; *Carr, 2020*; *Woodward et al., 2020*). Most recently, *Zanno & Napoli (2025)* presented evidence for two species of *Nanotyrannus* in the Hell Creek Formation (*N. lancensis* and *N. lethaeus*).

To aid in a taxonomic identification for the embedded tooth, comparisons of the preserved crown and denticle dimensions for MOR 1627 and published values from various sources (*Smith, Vann & Dodson, 2005*; *D'Amore & Blumenschine, 2012*; *Larson & Currie, 2013*; *Evans, Larson & Currie, 2013*; *DePalma et al., 2015*; *Larson, Brown & Evans, 2016*; *McLain et al., 2018*; *Currie & Evans, 2020*) (Tables S3–S4) for Hell Creek theropods were made. Because the embedded tooth is not complete, when the apicobasal (∼crown base height, CBH), mesiodistal (∼crown base length, CBL) and labiolingual (∼crown base width, CBW) dimensions of the tooth exceed corresponding values for complete tooth crowns for any taxon, that taxon can be eliminated from the list of possible candidates. Preserved length, width and height of the MOR 1627 tooth exceeds the reported crown heights for many Hell Creek theropods except for *Nanotyrannus* or *Tyrannosaurus* (Fig. 3). Denticle densities along the mesial and distal carinae are also consistent with the embedded tooth of MOR 1627 being from a tyrannosaurid. When the labiolingual and mesiodistal dimensions (taken at a crown height of five mm) of MOR 1627 are compared to corresponding dimensions for immature and adult *Tyrannosaurus* from maxillary and dentary positions (*Peterson & Daus, 2019*), the values for MOR 1627 plot closest to that of an adult maxilla (Fig. 3). Thus, MOR 1627 is most likely an adult *Tyrannnosaurus* maxillary tooth rather than an immature *Tyrannosaurus* or *Nanotyrannus* tooth. Denticle shape also suggests that MOR 1627 is a tyrannosaurid tooth (Table 2). Briefly, the embedded tooth of MOR 1627 lacks the disproportionately large and strong, apically hooked denticles characteristic of *Troodon* (*Peng, Russell & Brinkman, 2001*; *Sankey et al., 2002*). *Paronychodon* can also be quickly eliminated given the absence of longitudinal ridges along the exposed surface of the tooth and presence of well-developed denticles along both carinae (*Sankey et al., 2002*; *Larson, 2008*). The shape of the preserved tooth tip also lacks the characteristic isosceles shape of *Richardoestesia isosceles*, the denticles are much larger than that expected for *Richardoestesia*, and there is no noticeable disparity in mesial-distal denticle size or lack of mesial denticles (*Peng, Russell & Brinkman, 2001*; *Sankey et al., 2002*; *Larson, 2008*). Dromaeosaurids are generally unlikely candidates given that the embedded tooth lacks the mesio-distal denticle size disparity commonly observed for dromaeosaurid teeth (*Currie, Rigby Jr & Sloan, 1990*; *Sankey et al., 2002*; *Evans, Larson & Currie, 2013*), which is less pronounced in *Dromaeosaurus* (*Peng, Russell & Brinkman, 2001*) (Fig. 4). Thus, by process of elimination, the denticle morphology of MOR 1627 is most consistent with that of a tyrannosaurid.

Table 2 Comparison of key denticle characteristics of various theropods reported from the Hell Creek Formation and the embedded tooth of MOR 1627. Symbols: ?, condition of MOR 1627 cannot be directly compared to condition described in the literature; ~, condition of MOR 1627 partially matches the condition described in the literature; X, condition of MOR 1627 does not match the condition described in the literature; √, condition of MOR 1627 matches the condition described in the literature.

Source(s)	Taxa	Select characteristics		MOR 1627
Currie, Rigby Jr & Sloan (1990); *Sankey et al. (2002)*; *Sankey (2008)*; *Larson (2008)*	*Paronychodon*	longitudinal ridges on both labial and lingual surfaces	X	no longitudinal ridges on exposed side of tooth
		denticles along carinae are usually absent	X	denticles on both carinae
		when denticles are observed, they are poorly developed	X	denticles are well developed
Currie, Rigby Jr & Sloan (1990); *Peng, Russell & Brinkman (2001)*; *Sankey et al. (2002)*; *Sankey (2008)*	*Troodon*	disproportionately large denticles compared to the rest of the tooth	X	denticles are not disproportionately large
		sharply pointed denticles	X	denticle tips are rounded
	Troodon "large morph" specific	longitudinal ridges on labial and lingual surfaces	X	no longitudinal ridges on exposed side of tooth
		denticles on both carinae	√	
	Troodon "flat morph" specific	longitudinal ridges on labial and/or lingual surfaces	?	no longitudinal ridges on exposed side of tooth
		mesial denticles are typically absent but when observed are reduced in size compared to distal denticles	X	denticles on both carinae; mesial denticles are similar in size to distal denticles
		denticle tips are rounded to pointed	~	denticle tips are rounded
		denticles on both carinae	√	
Currie, Rigby Jr & Sloan (1990); *Peng, Russell & Brinkman (2001)*; *Sankey et al. (2002)*; *Sankey (2008)*; *Larson (2008)*	*Richardoestesia isosceles*	mesial denticles smaller than distal denticles	X	mesial denticles are similar in size to distal denticles
		small denticles that are closely spaced; high denticle density	X	large to moderate-sized denticles
		square-shaped denticles	X	chisel-like denticles

(*continued on next page*)

Table 2 (*continued*)

Source(s)	Taxa	Select characteristics		MOR 1627
Evans, Larson & Currie (2013)	*Acheroraptor*	longitudinal ridges on labial and lingual surfaces	X	no longitudinal ridges on exposed side of tooth
		denticles on both carinae	√	
		mesial denticles are smaller than distal denticles	X	mesial denticles are similar in size to distal denticles
		denticle tips are rounded	√	
		sub-rectangular distal denticles	~	both mesial and distal denticles are sub-rectangular
		distal denticles apically oriented	X	denticles are not apically oriented
DePalma et al. (2015) and based on Fig. 7 in (*DePalma et al., 2015*) for distal denticles	*Dakotaraptor*	denticles on both carinae	√	
		mesial denticles are smaller than distal denticles	X	mesial denticles are similar in size to distal denticles
		(distal) denticle tips are rounded	~	both mesial and distal denticles are rounded
		sub-rectangular (distal) denticles, being apicobasally shorter than mesiodistally long	~	both mesial and distal denticles are sub-rectangular
		(distal) denticles show apical inclination	X	denticles are not apically oriented
Currie, Rigby Jr & Sloan (1990); *Peng, Russell & Brinkman (2001)*; *Sankey et al. (2002)*; *Sankey (2008)*; *Currie & Evans (2020)*	*Saurornitholestes*	mesial denticles may be absent but when observed are reduced in size compared to distal denticles	X	denticles on both carinae; mesial denticles are similar in size to distal denticles
		chisel-like denticles	√	
		denticle tips are sharply pointed with the point directed apically; apical hook of denticle tips most noticeable on distal denticles located near tooth apex	X	denticle tips are rounded; denticles are not apically oriented
		blood grooves oriented parallel denticle long axis	?	no visible blood grooves

(*continued on next page*)

Table 2 (*continued*)

Source(s)	Taxa	Select characteristics	MOR 1627	
Currie, Rigby Jr & Sloan (1990); *Peng, Russell & Brinkman (2001)*; *Sankey et al. (2002)*; *Sankey (2008)*	*Dromaeosaurus*	denticles on both carinae	✓	
		mesial denticles are smaller than distal denticles; according to *Peng, Russell & Brinkman (2001)* size disparity is less pronounced	✓	
		chisel-like denticles	✓	
		denticle tips are not sharply pointed, with points being slightly inclined apically	X	denticle tips are rounded; denticles are not apically oriented
		blood grooves are shallow and poorly defined	∼	no visible blood grooves
		blood grooves oriented perpendicular to apicobasal tooth axis	?	no visible blood grooves
		longitudinal ridges on labial and lingual surfaces	X	no longitudinal ridges on exposed side of tooth
Sankey et al. (2002); *Sankey (2008)*	cf. ?*Dromaeosaurus* morphotype A	distal denticles may be absent but when observed are reduced in size compared to mesial denticles	X	denticles on both carinae; mesial denticles are similar in size to distal denticles
		chisel-like denticles	✓	
		denticle tips are not sharply pointed	X	denticle tips are rounded
Currie, Rigby Jr & Sloan (1990); *Peng, Russell & Brinkman (2001)*; *Smith (2005)*; *Larson (2008)*	Tyrannosauridae	denticles on both carinae	✓	
		mesial denticles are similar in size to distal denticles	✓	
		chisel-like denticles	✓	
		denticle tips are rounded	✓	
		denticles do not curve towards tooth tip	✓	
		blood grooves are long and oriented basally; best visible near base of tooth in lingual view between distal denticles	?	no visible blood grooves, base of tooth where grooves would be most visible not preserved

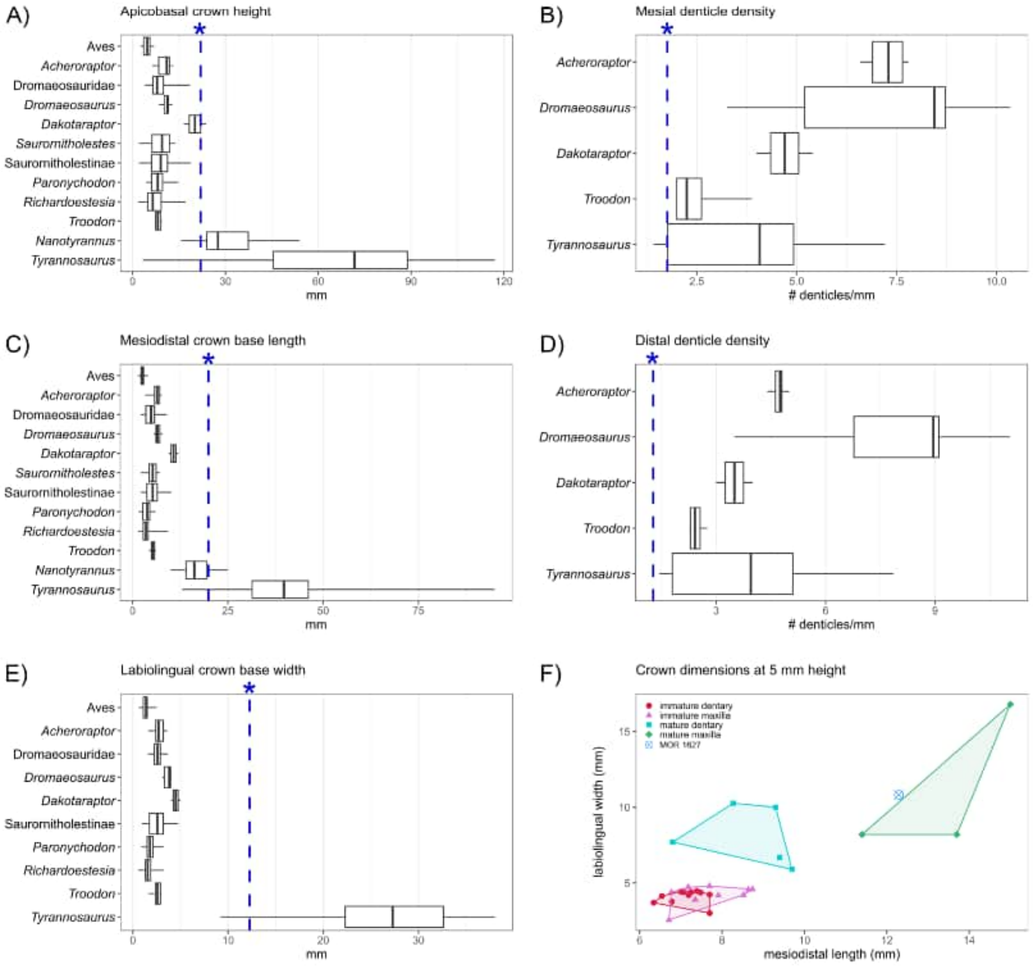

Figure 3 Select tooth crown measures for various theropods reported from the Hell Creek Formation. (A–E) depict common tooth crown dimensions considered in the literature. Dashed lines with asterisk indicates the corresponding values obtained for MOR 1627. (F) Comparison of mesiodistal and labiolingual dimensions of *Tyrannosaurus* tooth crowns at five mm crown height from *Peterson & Daus (2019)* to corresponding dimensions of MOR 1627. Abbreviations: CBL, mesiodistal crown base length; CBW, labiolingual crown base width; CH, apicobasal crown height. Note denticle densities shown for various theropods in B and D represent values taken from mid-way along the teeth to increase the number of taxa that could be compared whereas the denticle densities taken from MOR 1627 are apical.

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Position and bone of origin

The ventral orientation of the tip, slight curvature of the tip towards the anterior end of the skull suggests that the embedded tooth is either a maxillary or premaxillary tooth. In order for the tooth to be of dentary origin and for the tip to be directed ventrally, the theropod's head would need to be unnaturally held upside-down during the bite or the bite was delivered while the *Edmontosaurus* was positioned upside-down. The ovoid cross-sectional shape of the tooth further narrows the tooth to a maxillary or dentary origin, from positions 3 onwards (*i.e.*, non "mesial") as tyrannosaurid premaxillary teeth have

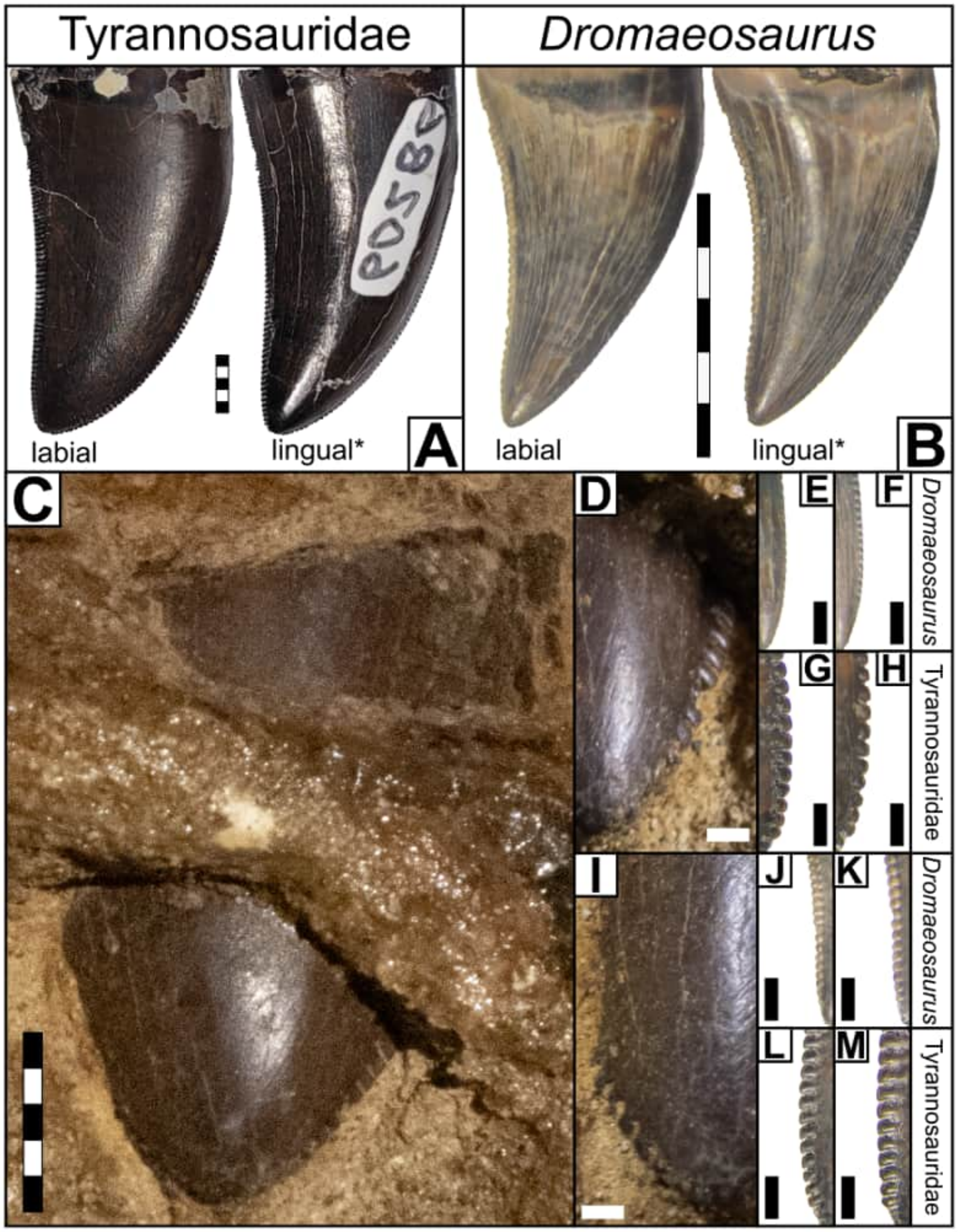

Figure 4 **Comparison of mesial (D–H) and distal (I–M) denticle morphology of lateral *Dromaeosaurus* (UALVP 55317), lateral tyrannosaurid (UALVP 60286) and MOR 1627.** (A) Lingual and labial views of isolated tyrannosaurid tooth. (B) Lingual and labial views of isolated *Dromaeosaurus* tooth. (C) Lateral view of embedded tooth of MOR 1627. (D) Close-up of mesial denticles of MOR 1627. Labial (E) and lingual (F) views of mesial denticles on *Dromaeosaurus* tooth. Labial (G) and (H) lingual views of mesial denticles on tyrannosaurid tooth. I) Close-up of distal denticles of MOR 1627. Labial (J) and lingual (K) views of distal denticles on *Dromaeosaurus* tooth. Labial (L) and lingual (M) views of distal denticles on tyrannosaurid tooth. Scale bars in mm. All views show teeth with apices pointing down. Note: all lingual views have been mirrored to match the orientation of the mesial and distal denticles of MOR 1627.

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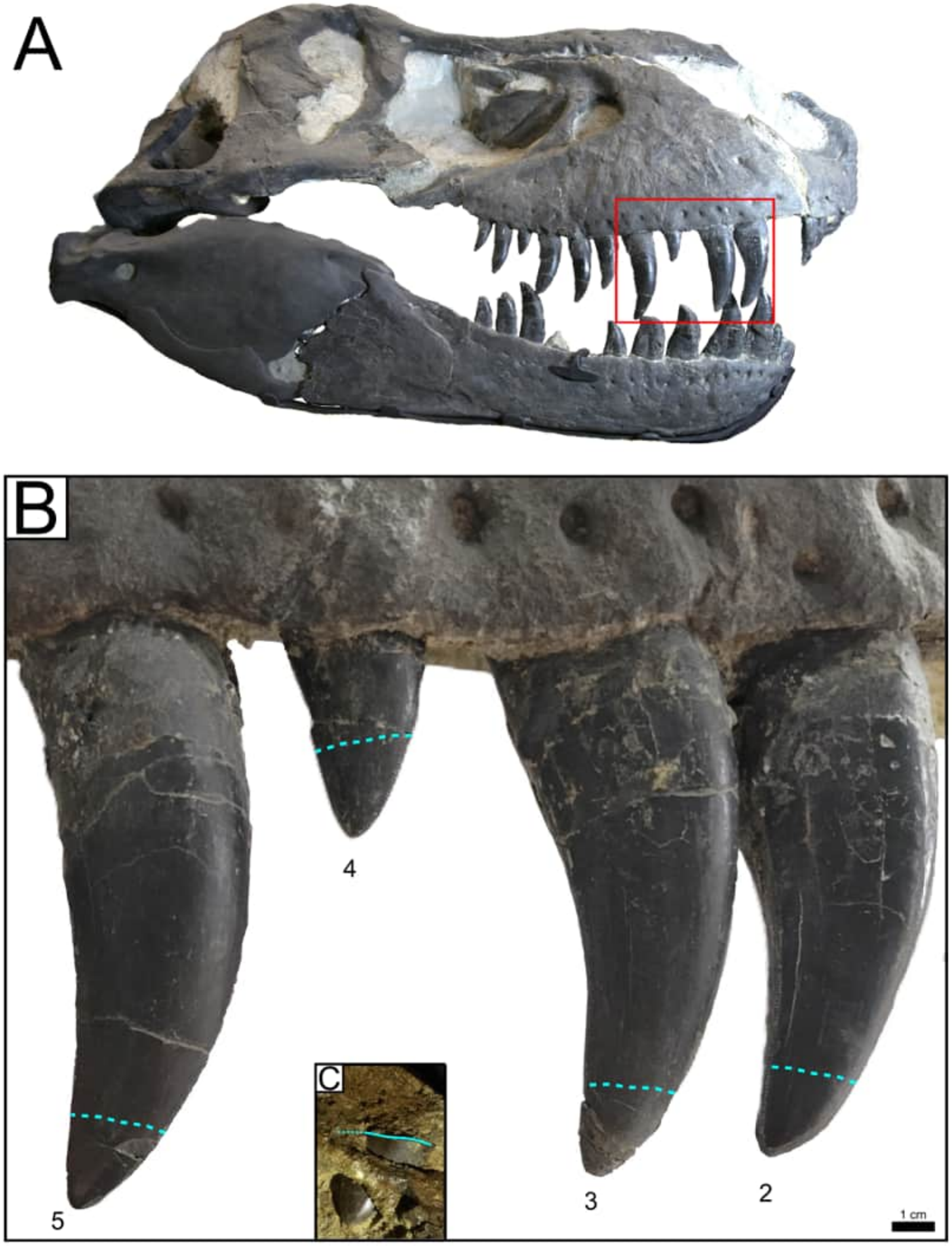

Figure 5 Comparison of embedded tooth in MOR 1627 to anterior and middle maxillary teeth of TMP 1981.006.0001. (A) Full skull in right lateral view with red box indicating the teeth shown in (B). (B) close-up of anterior and middle maxillary teeth in comparison to the embedded tooth of MOR 1627 (C) at the same scale. Lines in cyan indicate the maximal extent of the embedded tooth crown.

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a distinct D-shaped cross-section and the first two anterior ("mesial") maxillary/dentary teeth are more rounded in cross-section (*Samman et al., 2005*; *Smith, 2005*) (Fig. 5).

Animal size

Work by *D'Amore & Blumenschine (2012)* has suggested a relationship between apicobasal denticle dimensions and overall size. This relationship has been previously applied within the context of rake marks (*sensu Wyenberg-Henzler et al., 2024*) to identify minimum size of the tooth mark maker (*e.g.*, *McLain et al., 2018*). Here, we apply a similar approach for the embedded tooth in MOR 1627, using published denticle heights (Table S5) for *in-situ* teeth from maxillary and dentary tooth positions 3+ and corresponding skull lengths to identify animal size. We do not consider premaxillary teeth or the first two anterior tooth positions of the maxilla and dentary given the shape of the embedded tooth is not consistent with these teeth. A reduced major axis regression on estimates of quadrate height and skull length of *Edmontosaurus* specimens in the literature (Table S6) was conducted to approximate the full skull length of MOR 1627 from quadrate height. The full skull length of MOR 1627 is estimated between 0.79 m and 0.89 m while the skull length of the tyrannosaurid is estimated between 0.86 m and 1.12 m (Figs. 5 and 6). From estimates accumulated in *Carr (2020)*, this indicates that the animal likely weighed more than 1,807 kg (the estimate for LACM 23845 with a skull 0.8 m long) but less than 6,100 kg (the estimate for MOR 1125 with a skull 1.16 m long). This suggests the embedded tooth represents an animal over 500 kg heavier than what is estimated for the maximum mature weight of *N. lethaeus* (BMRP 2002.4.1; *Zanno & Napoli, 2025*) and is consistent with an identification of *Tyrannosaurus*.

Interpretation and implications

Predation or scavenging?

Whether *T. rex* and other tyrannosaurids were predators or scavengers has been a subject of disagreement in the literature citing various lines of evidence including tyrannosaurid physical attributes and interpretations of tooth marks/pathologies (*e.g.*, *Carpenter, 1998*; *Wegweiser, 2004*; *Carbone, Turvey & Bielby, 2011*; *Murphy, Carpenter & Trexler, 2013* *vs* *Horner & Lessem, 1993*; *Horner, 1994*; *Therrien et al., 2023* respectively). Given the nature of the fossil record and lack of perfect modern analogues, it is unlikely that this debate will be satisfactorily settled. Further complicating matters, a majority of modern carnivores lie on a predation-scavenger spectrum, rarely relying solely on either strategy to procure food and establishing which end of the spectrum modern carnivores are more inclined is extremely difficult (*DeVault, Rhodes Jr & Shivik, 2003*; *Holtz Jr, 2008*). Although some recent literature conceptualizes tyrannosaurids as both predators and scavengers (*e.g.*, *Holtz Jr, 2008*; *Horner, Goodwin & Myhrvold, 2011*; *Kane et al., 2016*), some publications still describe adult tyrannosaurids as "apex predators" (*e.g.*, *Therrien et al., 2023*).

It may be more pragmatic to conceptualize tyrannosaurids as both predators and scavengers. Further, being able to tease out which behaviour was more commonly practiced may be difficult with the information available for an extinct animal. The best that can probably be attained from the fossil record is how tyrannosaurids apprehended prey and manipulated carcasses. We note that the possibility of bite marks resulting from scavenging cannot be eliminated without direct evidence that the proposed prey animal was alive at the time of the bite (*e.g.*, pathologies resulting from failed predation attempts). Of the pathologies cited as evidence of tyrannosaurid predation, most examples are injuries to

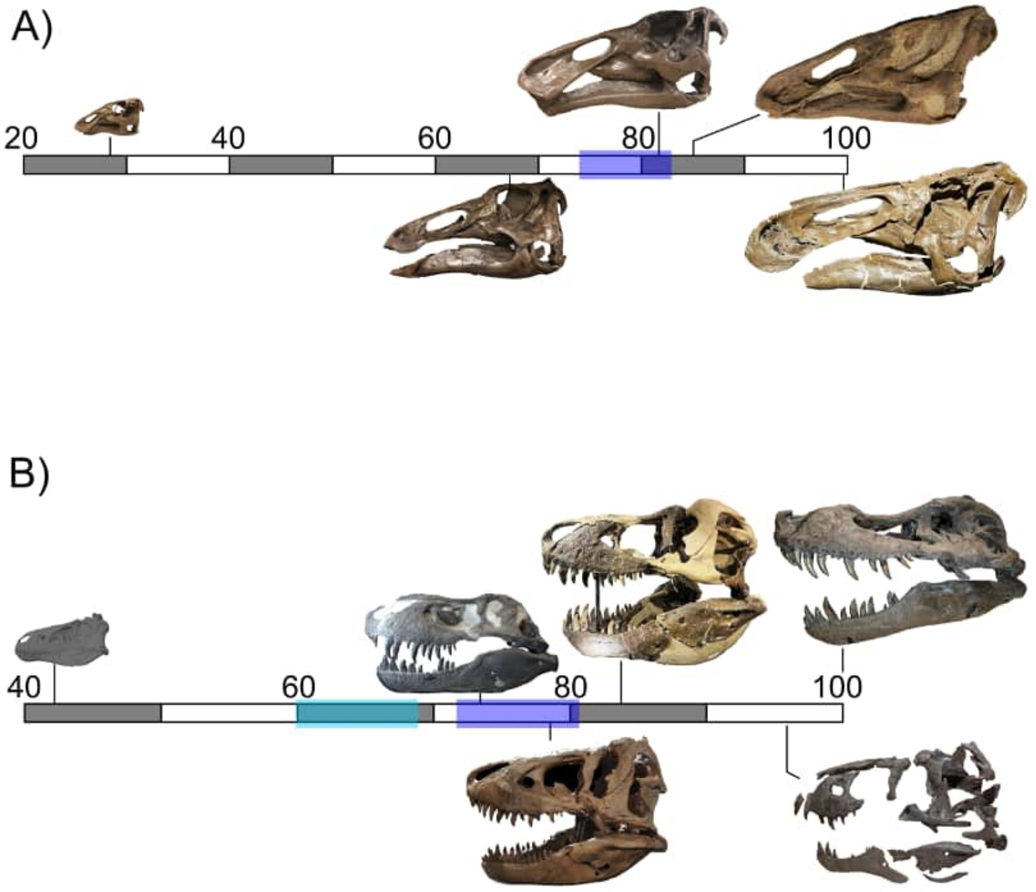

Figure 6 Estimated sizes of *Edmontosaurus* and *Tyrannosaurus* from reduced major axis regressions for MOR 1627. (A) Skull length of MOR 1627 (blue region) obtained from regression with quadrate height compared to other *Edmontosaurus* skulls (from left to right: composite of Prince Creek material, CMN 8509, MOR cast of DMNH 1493, ROM 57100, MOR 003). Axis numbers correspond to percent basal skull length of MOR 003. (B) Skull length of embedded tooth of MOR 1627 obtained from regression with apicobasal height of mesial (dark blue) and distal (light blue) denticles compared to other Hell Creek tyrannosaurid skulls (from left to right: CMNH 7541 (courtesy of the Cleveland Museum of Natural History), TMP 1981.006.0001, MOR 1125, MOR 980, RSM P2523.8 (courtesy of J. Milligan), FMNH PR2081). Axis numbers correspond to percent basal skull length of FMNH PR2081. Information regarding skull length, relative sizes and ontogenetic stages of specimens are available in Tables S7–S8.

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the tail of hadrosaurids (*Carpenter, 1998*; *Murphy, Carpenter & Trexler, 2013*; *DePalma et al., 2013*; but see also *Bertozzo et al., 2025*) with one example of damage to a rib of a lambeosaurine (*Wegweiser, 2004*) and another possible example that, if the pathology resulted from a bite, preserves evidence of an attack to the head of the ankylosaur *Tarchia* (*Tumanova et al., 2025*). Damage to the neural spines of the tail is interpreted as evidence of a bite delivered from behind while the hadrosaurid was trying to escape (*Carpenter, 1998*; *Murphy, Carpenter & Trexler, 2013*; *DePalma et al., 2013*). Although the etiology of the *Tarchia* skull pathologies is unclear, if they are indeed the result of a predation attempt by a tyrannosaurid, then the bite may have been delivered posterolaterally (*Tumanova* et al., 2025). However, Molnar (1998) suggested that tyrannosaurids, like modern canids, may have killed their prey by delivering a powerful crushing bite to the snout of a prey animal ultimately cutting off the airway and resulting in suffocation—a scenario virtually identical to the predation scenario proposed here that appears to be most consistent with the emplacement of the tooth in the skull of MOR 1627.

Embedded tooth and group 1 tooth marks

From the information presented above, the embedded tooth likely represents a middle-posteriorly positioned tooth from an adult *Tyrannosaurus*. The slight curvature of the tooth indicates that the mesial surface of the tooth is closer to the posterior end of the *Edmontosaurus* skull. Combined, this suggests that the tooth broke off during a bite that came from the front. The presence of tooth marks more anteriorly on the snout of MOR 1627 in the same region as the embedded tooth and on the same surface with a broadly similar orientation as the embedded tooth suggests that multiple teeth made contact during this bite. Under this scenario, the most anteriorly positioned contacting tooth would have penetrated the nasal while more posteriorly positioned teeth contacted the bone. The lack of bone remodelling in this region further indicates that the bite was inflicted at, near or after the time of death. Based on the behaviours of large carnivores, bites to the face, particularly to the snout of a herbivore, are inflicted in an attempt to gain control of a struggling prey animal during predation (mammals, crocodiles), to suffocate the prey animal (mammals), drown the prey animal (crocodiles) and/or to manipulate the carcass after the animal is already dead (*Emerson & Radinsky, 1980*; *Cleuren & De Vree, 2000*; *Karanth & Sunquist, 2000*; *Njau, 2006*; *Njau & Blumenschine, 2006*; *Van Valkenburgh, 2007*; *Wiesel, 2010*; *Westaway et al., 2011*; *Behrendorff, Belonje & Allen, 2018*).

Tooth marked specimens thought to be produced by tyrannosaurids are often attributed to carcass consumption (*Erickson & Olson, 1996*; *Fowler & Sullivan, 2006*; *Hone & Watabe, 2010*; *Hone, Tanke & Brown, 2018*; *Brown, Tanke & Hone, 2021*) rather than predation (*Carpenter, 1998*; *Wegweiser, 2004*; *Murphy, Carpenter & Trexler, 2013*). This is because most examples of tooth marks are very difficult to attribute to tyrannosaurids and subsequently interpret as evidence of predatory behaviour, especially given most tooth marks do not show signs of healing and so were produced at or near the time of death of the animal being fed upon making it hard to determine the sequence of events. Often, tooth mark interpretations involve whether predation or feeding is the most likely mechanism behind the production of those tooth marks but this is by no means definitive. Based on observations of modern carnivores, bites to the snout are typically inflicted as a means of prey capture or carcass manipulation (*Emerson & Radinsky, 1980*; *Cleuren & De Vree, 2000*; *Karanth & Sunquist, 2000*; *Njau, 2006*; *Njau & Blumenschine, 2006*; *Van Valkenburgh, 2007*; *Wiesel, 2010*; *Westaway et al., 2011*; *Behrendorff, Belonje & Allen, 2018*; *Somaweera et al., 2018*), rather than to consume flesh from the muzzle as relatively little flesh is found in this region; although, removal of flesh from this region is not entirely out of the realm of possibility (*Haynes, 1980*; *Haynes, 1982*; *Boaz et al., 2000*). Consumption of flesh from the snout region of a hadrosaurid is unlikely as very little flesh would have been present and the snout would have been covered with hard-to-digest, heavily keratinized skin and rhampotheca (*Fisher, 1981*; *Haynes, 1982*; *Novak et al., 2005*; *Bell, 2014*). Thus, two possible interpretations for MOR 1627 exist: emplacement during predation *versus* emplacement during carcass manipulation, either following predation or while scavenging. Falsification of the scavenging hypothesis would require evidence that the *Edmontosaurus* was alive when bitten, either through evidence of bone healing around an emplaced tooth (*e.g.*, *DePalma et al., 2013*) or other means. Although scavenging of MOR 1627 cannot be ruled out, here we argue that in the case of MOR 1627, predation is the more likely mechanism of emplacement for the embedded tooth given the directionality of the bite, the number and relative positioning of tooth marks and the level of articulation of the rest of the skull.

The positioning of the embedded tooth suggests the bite was directed from the front, while the *Edmontosaurus* was facing the tyrannosaurid. If the tooth was embedded during manipulation of the carcass after the animal was already dead, surely it would have been easier to grab the snout from either side with the upper jaws on one side of the skull and the lower jaws on the other side of the skull. Although rarely described, carrying behaviour in modern carnivores generally appears to leave multiple scores or pits on long bone diaphyses and multiple and/or paired marks on the cranium with punctures and/or furrows being relatively rare (*Pokines, 2021*). Mammalian carnivores tend to carry carcasses that are smaller compared to their body size, while larger carcasses tend to be consumed on-site or more mobile elements such as limbs (and rarely heads, which appear to be facilitated by grabbing the neck) are disarticulated and carried away to be eaten elsewhere (*Windell et al., 2019*). The penetrating nature of the tooth of MOR 1627 on the snout indicates high forces were exerted during the bite, something that is not expected during carrying behaviour after the animal has already been incapacitated. In modern carnivores, high bite forces are often delivered to dispatch prey or maintain control of a struggling animal from a position where the prey is unlikely to inflict damage *via* horns, tusks or teeth. Felids and spotted-tail quolls will apply a single, crushing bite to the head or throat of larger prey to reduce handling time and decrease the chances of injury (*Jones & Stoddart, 1998*; *Mondini & Muñoz, 2008*; *Meachen-Samuels & Van Valkenburgh, 2009*). In quolls the bite is delivered from behind to the braincase while in most felids, the attack begins from behind and the forelimbs are used to maintain a grip on the prey animal while the felid repositions itself to deliver a killing bite to the throat. Legless lizards will apply a similar strategy, biting relatively large prey by the head or neck and waiting for asphyxiation or exhaustion to occur (*Wall & Shine, 2007*; *Mukherjee & Heithaus, 2013*). In cooperative species, such as lions or African wild dogs, particularly for more dangerous prey with horns or tusks, bites to the head are used to control and/or drag down prey animals while other members of the group deliver the killing blow (*Kruuk & Turner, 1967*; *Mukherjee & Heithaus, 2013*). Other predators such as civets, Komodo monitors, and some canids will employ the opposite strategy, increasing handling time to reduce injury by delivering a series of quick bites to other areas of the body to exhaust prey or induce shock prior to applying the final crushing bite to the head or neck (*Eisenberg & Leyhausen, 1972*; *Jones & Stoddart, 1998*; *Therrien, Henderson & Ruff, 2005*; *Meachen-Samuels & Van Valkenburgh, 2009*). Crocodiles are ambush predators that will grab the legs or snout of a prey animal at the waters edge before dragging it into the water to be dispatched (*Heller, 1918*). Such attacks typically occur while the prey animal is drinking, facilitating a front-facing attack by the crocodile. Although a wide variety of hunting strategies can be seen in the animal kingdom, single bites to the head appear to be related to prey control or rapid dispatch of prey. Thus, the single, powerful bite to the snout emplacing the tooth in the nasal of MOR 1627 would appear to be more consistent with behaviours exhibited during predation rather than behaviours observed during feeding.

The high level of articulation of the skull also suggests predation. Most modern mammalian carnivores will consistently consume a carcass starting with higher economy areas, such as the abdominal cavity, and gradually consume lower economy areas, with the head usually being the last region consumed (*Blumenschine, 1986*; *Richardson, 1980*; *Selva et al., 2003*; *White & Diedrich, 2012*; *Haynes & Klimowicz, 2015*; *Drumheller et al., 2020*). Hyaenas are one of the few large mammalian carnivores that will occasionally deviate from this pattern, using multiple crushing bites to open the braincase to consume the brain relatively early on in the carcass consumption sequence (*Richardson, 1980*; *Blumenschine, 1986*; *Boaz et al., 2000*; *Wadley, 2020*). Comparison of encephalization quotients, which are calculated values quantifying relative brain and body masses, suggest a hyaena-like approach would have been less beneficial for dinosaurian carnivores. In modern megaherbivores such as blue wildebeest (*Connochaetes taurinus*, REQ = 26.7), impala (*Aepyceros melampus*, REQ = 27.0), African buffalo (*Syncerus caffer*, REQ = 23.6) and African elephants (*Loxodonta africana*, REQ = 73.2) (*Hurlburt, 1996*), values calculated using the reptilian encephalization quotient formula are much higher than those estimated for hadrosaurs (*Iguanodon*, REQ = 2.6; "*Anatosaurus*", REQ = 2.4; *Edmontosaurus*, REQ = 2.8) (*Hurlburt, 1996*; *Evans, 2005*). Consideration of previous examples attributed to cannibalistic scavenging would be consistent with the interpretation that tyrannosaurids followed a similar consumption sequence to modern, non-hyaenid carnivores wherein higher economy areas such as the abdominal cavity with cranial flesh being utilized later after most of the postcranial flesh has been consumed or decomposed (*Longrich et al., 2010*; *Hone & Tanke, 2015*). Under the typical carcass consumption sequence observed in modern carnivores, damage to the cranium is mainly concentrated around areas where the musculature is located (such as the coronoid process), occipital condyles and/or parietal bones and orbital margins (*Richardson, 1980*). The nasals of ungulates can also be heavily damaged or fragmented during carcass consumption. In some cases, the mandibles will also become disarticulated once the muscles and skin attaching them to the rest of the skull have been consumed (*Richardson, 1980*). Conversely, under a predation scenario, some damage might be inflicted during prey capture but the skull would remain otherwise unmodified as higher economy areas such as the internal organs in the abdominal cavity would be one of the first areas to receive attention after the animal was killed (*Richardson, 1980*; *Blumenschine, 1986*; *Selva et al., 2003*; *White & Diedrich, 2012*; *Drumheller et al., 2020*).

Other tooth marks

The spacing between the marks of group 2a on the left jugal are consistent with the spacing of tooth marks previously attributed to tooth marks produced by the premaxillary teeth (*Erickson & Olson, 1996*; *Fowler & Sullivan, 2006*; *Hone & Watabe, 2010*; *Rivera-Sylva, 2012*; *Drumheller et al., 2020*; *Lei et al., 2020*). *Hone & Watabe (2010)* have suggested that these teeth have been used in "scrape feeding" to remove flesh close to the bone surface. What exactly the tyrannosaurid was consuming in this region is unclear as the adductor musculature—the major source of flesh on the skull—would have been tucked underneath the jugal and postorbital (*Rybczynski et al., 2008*; *Holliday, 2009*; *Nabavizadeh, 2020a*; *Nabavizadeh, 2020b*) (Fig. 7) and accessing these muscles would have presumably moved these bones out of articulation. Recently, *Sharpe et al. (2025)* proposed another soft tissue in this region known as the exoparia which is reconstructed as extending from the lateral surface of the jugal flange to the surangular. Removal of this structure would have left the skull largely articulated if most of the adductor musculature underneath was largely intact. However, the tooth marks in group 2a are located near the posterior margin of the postorbital fenestra which is positioned more dorsally than the flange of the jugal where the exoparia is reconstructed (Fig. 7). One possible, albeit less likely explanation for this is the exoparia extends higher on the jugal than originally proposed. A more likely explanation is that the tooth marks in group 2a were produced by teeth of the right premaxilla contacting the bone surface while teeth of the left premaxilla removed the exoparia.

Spacing between tooth marks of groups 2b, 3, 4 and 5 are much greater than those seen for group 2a marks (Fig. 1). Although this could suggest that these tooth marks were produced by more lateral teeth, a scenario where teeth from both premaxillae are contacting the bone can also be envisioned. The stage of tooth eruption, angle at which teeth contact bone and the surface topography of the bone will theoretically impact what teeth contact the bone surface (*Hone & Rauhut, 2010*; *Lei et al., 2020*). It is possible that teeth from both premaxillae or at the very least anterior teeth from opposite sides of the skull were involved in the production of group 3–5 tooth marks but only three teeth made actual contact with the bone surface—one tooth from one premaxilla and two teeth from the other or one anterior maxillary tooth on one side and two teeth from the premaxilla on the opposite side. What teeth produced the remaining tooth marks is uncertain given ascertaining tooth spacing is impossible from a single tooth mark. Given the proximity of group 5 tooth marks to m. pterygoideus ventralis, it is possible that these tooth marks were inflicted while feeding on this muscle (*Rybczynski et al., 2008*; *Holliday, 2009*; *Nabavizadeh, 2020a*; *Nabavizadeh, 2020b*) (Fig. 7). The close proximity of the remaining tooth marks on the right mandible to possible articulation points of various adductor muscles (*Rybczynski et al., 2008*; *Holliday, 2009*; *Nabavizadeh, 2020a*; *Nabavizadeh, 2020b*) (Fig. 7), would also suggest that these tooth marks were produced during feeding on the adductor musculature. However, it is hard to imagine entire muscle masses being removed without disturbing the overlying jugal in most cases so these tooth marks may either represent removal of only portions of the muscles or consumption of soft tissue other than the adductor musculature. It is also possible that some of the tooth marks concentrated on the coronoid process of the right mandible are associated with the removal of the exoparia which extends from the lateral surface of the jugal flange to the surangular (*Sharpe et al., 2025*) and could have been removed without disturbing the jugal. Although *Sharpe et al. (2025)* were unable to determine the exact nature of the exoparia, targeted feeding on the exoparia suggests it had higher nutritive value which would implicate the exoparia was muscular rather than ligamentous in nature. Alternatively, the relatively shallow nature of the exoparia could

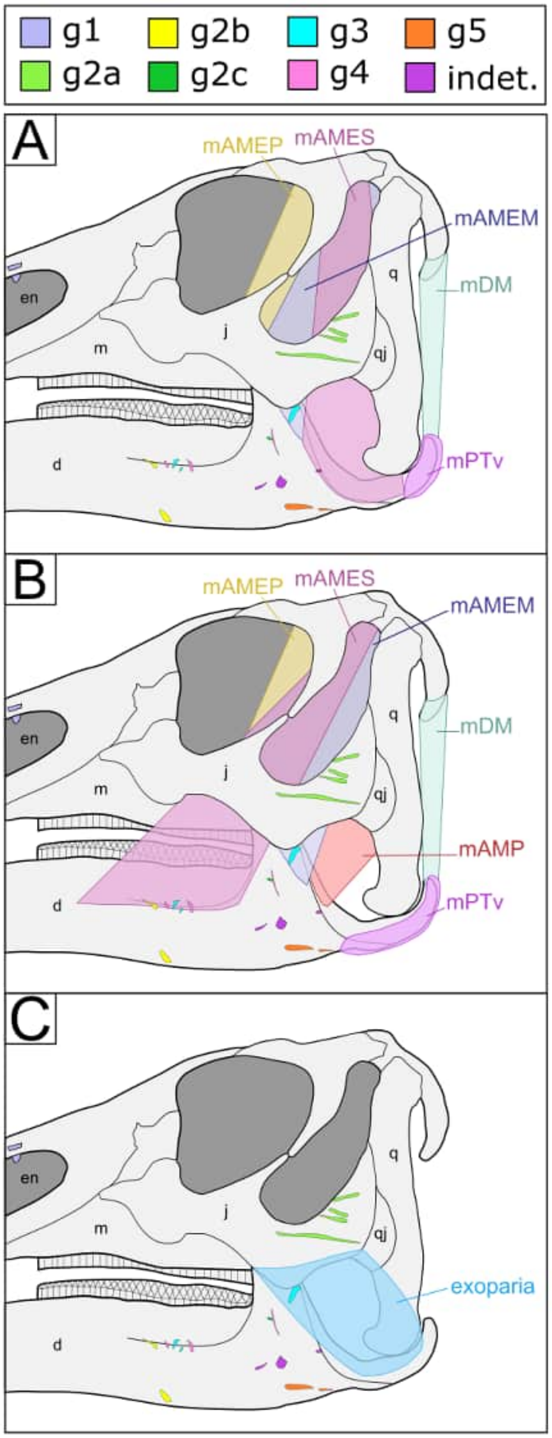

Figure 7 **Location of tooth marks on the skull of MOR 1627 relative to the approximate location of adductor muscles and the exoparia.** Tooth marks from the right side of the skull have been mirrored and superimposed on the left side of the skull. (A) Reconstruction assuming attachment of mAMES to the coronoid process (following *Rybczynski et al., 2008*; *Holliday, 2009*; *Nabavizadeh, 2020b*). (continued on next page…)

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Figure 7 (…continued)
(B) Reconstruction assuming attachment of mAMES to the labial dentary ridge (following *Nabavizadeh, 2020a*). (C) Reconstruction showing the approximate position of the exoparia (following *Sharpe et al., 2025*). Abbreviations: mPTv, m. pterygoideus ventralis; mAMEP, m. adductor mandibulae externus profundus; mAMES, m. adductor mandibulae externus superficialis; mAMEM, m. adductor mandibulae externus medialis; mAMP, m. adductor mandibulae posterior.

have made it particularly easy to remove thus making the benefit outweigh the cost of its removal.

The cracking observed on the left and right jugals and the right mandible that parallel the bone fiber is consistent with subaerial exposure prior to burial (*Behrensmeyer, 1978*; *Pokines et al., 2018*). The level of cracking on the left jugal is far less pronounced than that on the right jugal and mandible, suggesting that the skull was positioned left-side-down, leaving it exposed for a shorter period of time. The presence of this cracking on both sides of the skull indicates that skull of MOR 1627 would have been sitting exposed to the surface for some period of time, likely with the right side of the skull exposed for longer than the left (*Behrensmeyer, 1978*). Whether this exposure was before or after the majority of the tooth marks on the skull were inflicted cannot be determined as there is little difference in the physical appearance of tooth marks inflicted prior to weathering and those inflicted on the surface of weathered bone (*Vachirawongsakorn, 2019*).

Carcass abandonment?

The high level of articulation of the skull also suggests something about the nature of the skull at the time it was buried. As previously discussed, the level of articulation suggests that some, if not most of the adductor musculature had not been consumed by hungry carnivores. This adductor musculature could have also prevented disturbance of the elements during burial in a higher energy environment, as indicated by MOR 1627 being recovered from a sandstone. It therefore appears likely that at least some of the adductor musculature was left intact at the time of burial. Although it is possible the skull was buried before carnivores could have consumed this region, it seems odd that the exoparia and possibly some of the other adductor muscles were consumed while the majority of the adductor musculature remained untouched. Presumably, removal of the jugal and quadratojugal to access the underlying musculature would have been relatively easy for a tyrannosaurid to have accomplished if it were sufficiently motivated given the deeper adductor musculature (*e.g.*, mAMEP and mAMEM) would have accounted for a majority of the flesh on the skull. Although it is possible for the skull to have been buried before the skull could have been disarticulated to access this musculature, the weathering present on the jugal suggests the skull sat subaerially exposed for some period of time prior to burial. Considering the behavior of modern carnivores, we propose that MOR 1627 is an example where the carcass of a predated animal had been mostly, but not completely, utilized before it was abandoned. Given tyrannosaurids appear to have followed the typical carcass consumption sequence of modern non-hyaenid carnivores (*e.g.*, *Hone & Tanke, 2015*), more superficial tissue from the skull (*e.g.*, the exoparia) was likely removed after most of the postcranial tissue had been utilized, producing the remaining tooth marks on MOR

1627. During the process of carcass consumption, modern carnivores will disarticulate, fragment and/or carry off parts of the postcranial skeleton away from the main carcass, especially when competition between carnivores, either of the same or different species, is higher (*Capaldo & Peters, 1995*; *Haynes & Klimowicz, 2015*; *White & Diedrich, 2012*; *Wadley, 2020*). Of particular significance are observations regarding the consumption of a large kudu carcass reported by *Wadley (2020)*. After a few weeks of being fed upon by carnivores, all that remained were a few fragments of the postcranial skeleton (about 5.5 g worth) and the skull. Although the skull had been dragged away from its original position, the skull was virtually untouched and the brains had not been fed upon despite the presence of hyaenas at the site. If MOR 1627 underwent a similar process before it was abandoned, only a few postcranial fragments would have been present and could have easily washed away during burial. There is also precedence in the modern record for the same carnivores to repeatedly visit a kill site over a period of time before abandoning the skull (sometimes with the neck also articulated) with relatively little tooth marking or flesh removal (*Richardson, 1980*; *Haynes, 1982*; *Capaldo & Peters, 1995*; *Haglund, 1997*; *Haynes & Klimowicz, 2015*; *Wadley, 2020*). Given the spacing of the tooth marks on the left jugal and right mandibles are consistent with that of a *Tyrannosaurus*, and the embedded tooth is also that of a *Tyrannosaurus*, it is plausible for MOR 1627 to represent a scenario where the same animal, or group of animals, repeatedly visited the carcass over a period of time before abandoning the skull, with most of the adductor musculature intact, in favor of a fresher carcass.

CONCLUSIONS

In summary, MOR 1627 preserves evidence most consistent with the *Edmontosaurus* being predated on by a *Tyrannosaurus* with a skull approximately one meter long and subsequent subaerial exposure and consumption of the carcass. Predation is the most consistent explanation for the high level of articulation, relative completeness and lack of tooth marks in the braincase region observed. Conversely, the lack of postcranial material combined with the tooth marks on the left jugal and right mandible are more consistent with consumption of some of the soft tissue on the skull either prior to or following subaerial exposure of the skull before the skull was ultimately buried. Together, these observations suggest that MOR 1627 could have been the result of prolonged carcass utilization and subsequent carcass abandonment following a predation event.

Institutional Abbreviations

CMN	Canadian Museum of Nature (Ottawa, ON)
CMNH	Cleveland Museum of Natural History (Cleveland, OH)
DMNH	Denver Museum of Nature and Science (Denver, CO)
FMNH PR	Field Museum of Natural History (Chicago, IL)
MOR	Museum of the Rockies (Bozeman, MT)
ROM	Royal Ontario Museum (Toronto, ON)
RSM	Royal Saskatchewan Museum (Regina, SK)
TMP	Royal Tyrrell Museum of Palaeontology (Drumheller, AB)

UALVP	University of Alberta Laboratory of Vertebrate Palaeontology (Edmonton, AB)

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Taia C.A. Wyenberg-Henzler conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- John B. Scannella conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the article, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The raw data and code are available in the Supplemental Files.

Raw CT scan data and 3D model derived from this scan data are available at Morphosource:

– Media 000773842: MOR 1627 CT Image Series:
https://doi.org/10.17602/M2/M773842.
– Media 000774156: MOR 1627 3D Model:
https://doi.org/10.17602/M2/M774156.

Supplemental Information

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