Feeding traces attributable to juvenile *Tyrannosaurus rex* offer insight into ontogenetic dietary trends

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Theropod dinosaur feeding traces and tooth marks provide paleobiological and paleoecological implications for social interactions, feeding behaviors, and direct evidence of cannibalism and attempted predation. However, ascertaining the taxonomic origin of a tooth mark is largely dependent on both the known regional biostratigraphy and the ontogenetic stage of the taxon. Currently, most recorded theropod feeding traces and bite marks are attributed to adult theropods, making the presence of juvenile and subadult tooth marks largely absent from the literature. Here we report on the first feeding traces attributable to a late-stage juvenile *Tyrannosaurus rex* on a caudal vertebra of a hadrosaurid dinosaur. The dimensions and spacing of the traces were compared to the dentition of *Tyrannosaurus rex* maxillae and dentaries of different ontogenetic stages. These comparisons reveal that the tooth marks present on the vertebra closely match the maxillary teeth of a late-stage juvenile *Tyrannosaurus rex* specimen histologically determined to be 11-12 years of age. These results demonstrate for the first time that late-stage juvenile and subadult tyrannosaurs were already utilizing the same large-bodied food sources as adults, indicating less niche partitioning than previously hypothesized. Further identification of tyrannosaur feeding traces coupled with experimental studies of the biomechanics of tyrannosaur bite forces from younger ontogenetic stages may reveal dynamic dietary partitioning and ecological roles of *Tyrannosaurus rex* throughout ontogeny.

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Abstract

Theropod dinosaur feeding traces and tooth marks provide paleobiological and paleoecological implications for social interactions, feeding behaviors, and direct evidence of cannibalism and attempted predation. However, ascertaining the taxonomic origin of a tooth mark is largely dependent on both the known regional biostratigraphy and the ontogenetic stage of the taxon. Currently, most recorded theropod feeding traces and bite marks are attributed to adult theropods, making the presence of juvenile and subadult tooth marks largely absent from the literature. Here we report on the first feeding traces attributable to a late-stage juvenile *Tyrannosaurus rex* on a caudal vertebra of a hadrosaurid dinosaur. The dimensions and spacing of the traces were compared to the dentition of *Tyrannosaurus rex* maxillae and dentaries of different ontogenetic stages. These comparisons reveal that the tooth marks present on the vertebra closely match the maxillary teeth of a late-stage juvenile *Tyrannosaurus rex* specimen histologically determined to be 11-12 years of age. These results demonstrate for the first time that late-stage juvenile and subadult tyrannosaurs were already utilizing the same large-bodied food sources as adults, indicating less niche partitioning than previously hypothesized. Further identification of tyrannosaur feeding traces coupled with experimental studies of the biomechanics of tyrannosaur bite forces from younger ontogenetic stages may reveal dynamic dietary partitioning and ecological roles of *Tyrannosaurus rex* throughout ontogeny.

Introduction

Bite marks and feeding traces attributable to theropods dinosaurs provide important insight on behavior, physiology, and paleobiology. Furthermore, the presence of bites and feeding traces on fossilized bone represents a valuable aspect of paleoecology; the interaction between two organisms as preserved in both traces and body fossils. Bite marks and feeding traces are relatively common in the fossil record, and are widely reported for theropod dinosaurs. Such traces have provided evidence of gregariousness and social interactions (Tanke and Currie, 1998; Bell and Currie, 2009; Peterson et al., 2009; Currie and Eberth, 2010), feeding behaviors and bone utilization (Erickson and Olson, 1996; Chure et al., 1998; Hone and Watabe, 2010; Hone and Rauhut, 2010), direct evidence of attempted predation (DePalma et al., 2013), and cannibalism (Longrich et al., 2010; Mclain et al., 2018).

Despite the abundant record of theropod tooth marks, ascertaining the origins of feeding traces and bite marks can be challenging; determining the species responsible for the marks and establishing whether tooth marks are the result of active predation or scavenging largely depends on the taphonomic setting of the skeletal elements, the presence of shed teeth, and the location of the traces on the specimen in question (Hunt et al, 1994; Bell and Currie, 2009; Hone and Rauhut, 2010). However, most recorded cases of theropod feeding or the presence of bite marks are attributed to adult theropods, leaving the presence of juvenile and subadult tooth marks largely absent from the literature and discussion.

Here we report on the presence of feeding traces on the caudal vertebra of a hadrosaurid (BMR P2007.4.1, "Constantine"). Based on the shape and orientation of the traces, and the known phyla of the Hell Creek Formation, they are interpreted to be feeding traces attributable to a large theropod dinosaur, such as *Tyrannosaurus rex* (Erickson and Olson, 1996; Horner et al., 2011). By comparing the dimensions and spacing of the traces with the maxillae and dentaries of specimens of *Tyrannosaurus rex* of different ontogenetic stages, we interpret these tooth marks to be feeding traces from a juvenile *Tyrannosaurus rex* and discuss the insights the specimen provides for juvenile tyrannosaur feeding behavior.

Institutional Abbreviations - BHI, Black Hills Institute of Geologic Research, Hill City, SD, USA; **BMR**, Burpee Museum of Natural History, Rockford, IL, USA.

Geologic Setting

Specimen BMR P2007.4.1 ("Constantine") is a partial hadrosaurid skeleton collected from the Upper Cretaceous Hell Creek Formation of Carter County, southeastern Montana in the Powder River Basin (Figure 1). This specimen was collected on public lands under BLM Permit #M96842- 2007 issued to Northern Illinois University and is accessioned at the Burpee Museum of Natural History in Rockford, IL. Exact coordinates for the location are on file in the paleontology collections at the Burpee Museum of Natural History (BMR), where the specimen is reposited.

The collection locality is composed of a 4m fine-grained, gray-tan lenticular sandstone laterally adjacent to a siltstone unit (Figure 2). The sandstone lacks bedforms, resulting from either a) rapid accumulation (resulting in a lack of sedimentary structures), or b) sedimentary structures that were obliterated by later currents or bioturbation, and is rich in rounded and weathered microvertebrate remains. The site is stratigraphically positioned approximately 44 m above the underlying Fox Hills – Hell Creek contact and overlies 0.5 m of siderite, which sits above a 5 m blocky mudstone. Grains are subrounded to subangular. Microvertebrate and fragmented macrovertebrate fossils are abundant and heavily rounded and abraded (Peterson et al., 2011). The bone-bearing unit is lenticular in shape and is surrounded laterally by a siltstone unit. The fine-grained composition suggests a channel-fill deposit, overlying a floodplain deposit (Murphey et al., 2002; Peterson et al., 2011). The taphonomic distribution of the elements and their stratigraphic position suggests the skeleton was subaerially exposed on a floodplain for a considerable period of time prior to burial, allowing for weathering, disarticulation, and removal of many skeletal elements.

Materials & Methods

Specimen BMR P2007.4.1 ("Constantine") consists of weathered pelvic elements (sacrum, left and right ilia), three dorsal vertebrae and two proximal caudal vertebrae (Figure 3, Table 1). The dorsal vertebrae were too weathered for collection, though their dimensions and relative locations within the quarry assemblage were measured and documented. Additionally, a series of heavily-weathered bone fragments and a small shed theropod tooth (e.g. *Saurornithoides sp.*) were also collected.

Based on stratigraphic position of BMR P2007.4.1 coupled with morphological characteristics such as 1) the shallow morphology of the ilium, 2) the hadrosaur-like antitrochanter dorsal to the ischial peduncle, and 3) a ~23o preacetabular process in lateral view relative to the main body, BMR P2007.4.1 is attributable to the Late Cretaceous hadrosaurid *Edmontosaurus* (i.e. Brett-Surman and Wagner, 2007; Campione, 2014).

The centra of the two caudal vertebrae lack any evidence for hemal arch attachments, suggesting they are among the more cranial-positioned caudal vertebrae, such as C1-C4 (Campione, 2014). One of the caudal vertebra possesses three v-shaped punctures on the ventral surface of the centrum (Figure 4A-E). The punctures penetrate 5 mm deep, are spaced 68 mm apart from their apical centers, show no signs of healing, and are inferred to have been created post-mortem as feeding traces (e.g. Noto et al., 2012; Hone and Tanke, 2015; Mclain et al., 2018). By comparing the shape and orientation of the traces, they are hypothesized to be bite marks from a large theropod dinosaur, such as *Tyrannosaurus rex* (Erickson and Olson, 1996).

To test this hypothesis, the punctures on the caudal vertebra of BMR P2007.4.1 were first coated in ReboundTM 25 platinum-cure silicone rubber (Smooth-On) in order to make a silicone peel of the punctures in order to better visualize the morphology and dimensions of the teeth responsible for the traces (Figure 5A-B). These "teeth" were then compared with the dental dimensions and spacing of two *Tyrannosaurus* maxillae and dentaries. To approximate the ontogenetic stage of the tyrannosaur, a late-stage juvenile specimen (BMR P2002.4.1, "Jane") histologically determined to be approximately 11-12 years old at the time of death (Erickson et al., 2006) that possesses laterally compressed, sharp crowns, and a mature specimen (BHI 3033, "Stan") with robust, blunt crowns were utilized.

All specimens were digitized via triangulated laser texture scanning with a NextEngine 3D Laser Scanner, capturing data at seven scanning divisions in high-definition (2.0k points/in2). The resulting digital models were built with the NextEngine ScanStudio HD Pro version 2.02,

and finalized as STL models (Supplemental Figures S1 and S2). Scanning was conducted at the Department of Geology at the University of Wisconsin-Oshkosh in Oshkosh, WI.
The tooth spacing of both adult and late-stage juvenile tyrannosaur maxillae and dentaries were measured for both immediately-adjacent teeth and alternating *Zahnreihen* tooth replacement patterns, and compared with the spacing of the punctures (Figure 6A-B). Furthermore, the cross-sectional morphology of adult and late-stage juvenile tyrannosaur maxillae and dentaries were measured labiolingually and mesiodistally at a 5 mm apical depth for each tooth crown, and plotted with measurements from the punctures found on BMR P2007.4.1 (Figure 7).

Results

The mesiodistal width measurements from the silicone peel taken from BMR P2007.4.1 average 7.8 mm and the labiolingual depth average was 5.2 mm. Maxillary and dentary teeth of the adult *Tyrannosaurus* (BHI 3033) were found to be too large and widely spaced to have produced the punctures (Figures 7,8A,B; Table 2A-C). For BHI 3033, the average dentary tooth crown mesiodistal width at 5 mm depth was 7.13 mm, and the average dentary tooth crown labiolingual depth at 5 mm was 4.10 mm. The average maxillary crown mesiodistal width at 5 mm were 7.72 mm, and the average maxillary crown labiolingual depth at 5 mm averaged to 4.21 mm.

However, the teeth of BMR P2002.4.1 produced similarly shaped punctures at 5 mm apical depth (Figure 7, 9; Table 2B-C). The puncture measurements taken from the peel, BMR P2007.4.1 demonstrate a mesiodistal width and labiolingual depth consistent with the measurements taken from the maxillary and dentary teeth of the late-stage juvenile *Tyrannosaurus*. When plotted against the mesiodistal width and labiolingual depth of the maxillary teeth, measurements from the peel taken from BMR P2007.4.1 fall well within the cluster radius created by the late-stage juvenile *Tyrannosaurus*, BMR P2002.4.1 (Figure 7). Furthermore, the inferred crown spacing of the punctures closely matched those of the late-stage juvenile tyrannosaur maxilla (Table 3A-B).

Discussion and Conclusions

The dimensions and spacing of the punctures closely matches the maxillary teeth of BMR P2002.4.1, a late-stage juvenile (11-12 yr old) tyrannosaur which incidentally itself possesses morphologically similar craniofacial lesions previously interpreted as a conspecific bite (Peterson et al., 2009). While bite marks resulting from active predation cannot easily be distinguished from postmortem feeding traces, the ventral position of the punctures on the caudal centrum of BMR P2007.4.1 suggests that the feeding was taking place postmortem with the hadrosaur already on its side (Chure et al., 1996). The afflicted vertebra is from the cranial-most caudal sequence where a significant muscle mass would have been associated en vivo, suggesting relatively early-stage carcass consumption and reflecting postmortem feeding behaviors.

While feeding traces and bite marks attributed to mature tyrannosaurids are well-documented in common Late Cretaceous taxa such as hadrosaurids and ceratopsians (i.e. Fiorillo, 1991; Erickson et al., 1996a,b; Jacobsen, 1998; Farlow and Holtz, 2002; Fowler and Sullivan, 2006; Peterson et al., 2009; Bell and Currie, 2010; Longrich et al., 2010; Fowler et al., 2012; DePalma et al., 2013, Mclain et al., 2018), the first identification of juvenile tyrannosaur feeding traces adds insight into the role of juvenile theropods in Cretaceous ecosystems. The identification of penetrating bite marks attributable to not only *Tyrannosaurus rex*, but an individual of 11-12 years of age can potentially allow for the determination of the ontogeny of bite force in *Tyrannosaurus rex* and for comparison with other theropods (e.g. Barrett and Rayfield, 2006, Gignac et al., 2010; Bates and Falkingham, 2012).

The bite forces of an adult *Tyrannosaurus rex* have been estimated to have been between 8,526—34,522 N, coupled with tooth pressures of 718—2,974 MPa, and a unique tooth morphology and arrangement to promote fine fragmentation of bone during osteophagy (Gignac and Erickson, 2017). However, juvenile *T. rex*, such as BMR P2002.4.1 have much narrower and blade-like tooth morphologies and were unlikely to have been able to withstand similar bite forces at this ontogenetic stage. Bates and Falkingham (2012) estimate a maximum bite force for BMR P2002.4.1 at 2,400-3,850 N, and suggest that an increase in bite force during growth could indicate a change in feeding behavior and diet while approaching adulthood.

Observation on extant crocodilians have documented a wide variety of dietary partitioning during ontogeny (e.g. Tucker et al., 1996; Platt et al., 2006; Platt et al., 2013). In the American Crocodile (*Crocodylus acutus*), hatchling and small juveniles have a dietary overlap of over 80%, commonly feeding upon insects and crustaceans (Platt et al., 2013). Alternatively, larger juveniles, subadults, and adults possess a dietary overlap of over 75%, consisting of more birds, mammals, fish, and other reptiles (Platt et al., 2013). Comparable ontogenetic dietary partitions were also observed in Morelet's Crocodile (*Crocodylus moreletii*) (Platt et al., 2006), and in Australian freshwater crocodiles (*Crocodylus johnstoni*) (Tucker et al., 1996).

While bite marks and feeding traces attributable to younger juvenile and hatchling tyrannosaurs have not yet been identified, the punctures present on the caudal vertebra of BMR P2007.4.1 provide direct evidence that late-stage juvenile *Tyrannosaurus rex* such as BMR P2002.4.1 possessed a similar diet as adults. Despite not yet possessing the same feeding mechanisms of an adult *Tyrannosaurus rex* (i.e. bone-crushing and osteophagy), the punctures present on BMR P2007.4.1 demonstrate that late-stage juvenile and subadult tyrannosaurs were already biomechanically capable of puncturing bone during feeding, and were doing so without the large, blunt dental crowns of adults. Further identification of tyrannosaur feeding traces from different ontogenetic stages coupled with experimental studies of the biomechanics of tyrannosaur bite forces may reveal more insight into dynamic dietary partitioning and ecological role of *Tyrannosaurus rex* throughout ontogeny.

Acknowledgements

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Figure 1

Discovery location of BMR P2007.4.1

Locality map showing the geographic location of specimen BMR P2007.4.1 in Carter County, Montana.

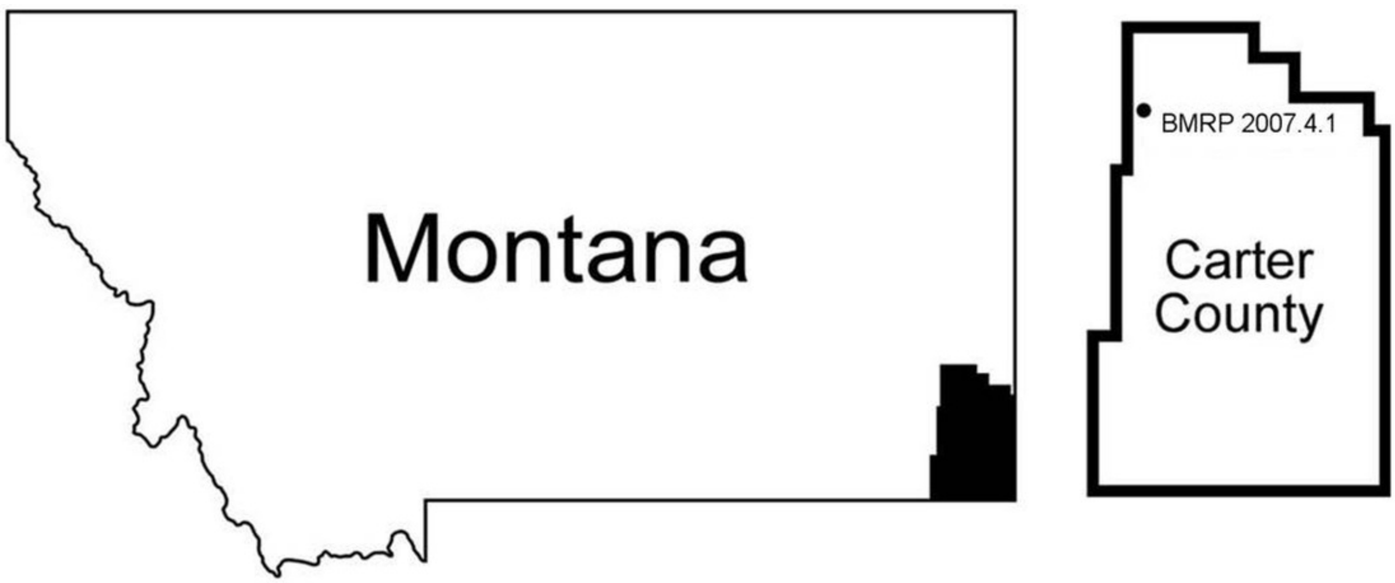

Figure 2

Stratigraphic column of the "Constantine" Quarry.

Stratigraphy of the BMR P2007.4.1 "Constantine" Quarry.

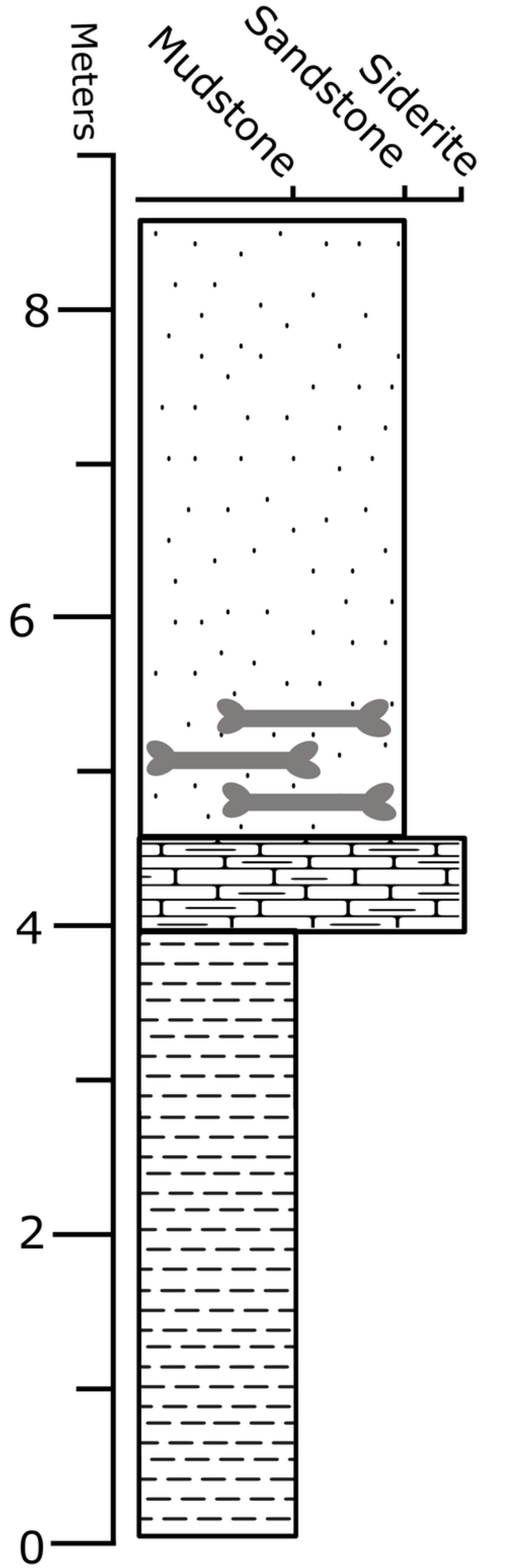
Meters
Mudstone
Sandstone
Siderite
8
6
4
2
0

Figure 3

Map of the BMR P2007.4.1 "Constantine" Quarry.

Dorsal vertebrae (field numbers CON-2007-010, CON-2007-011, and CON-2007-012) were too weathered for collection, though their relative locations were mapped. Note the relative association of dorsal and caudal vertebrae, and pelvic elements.

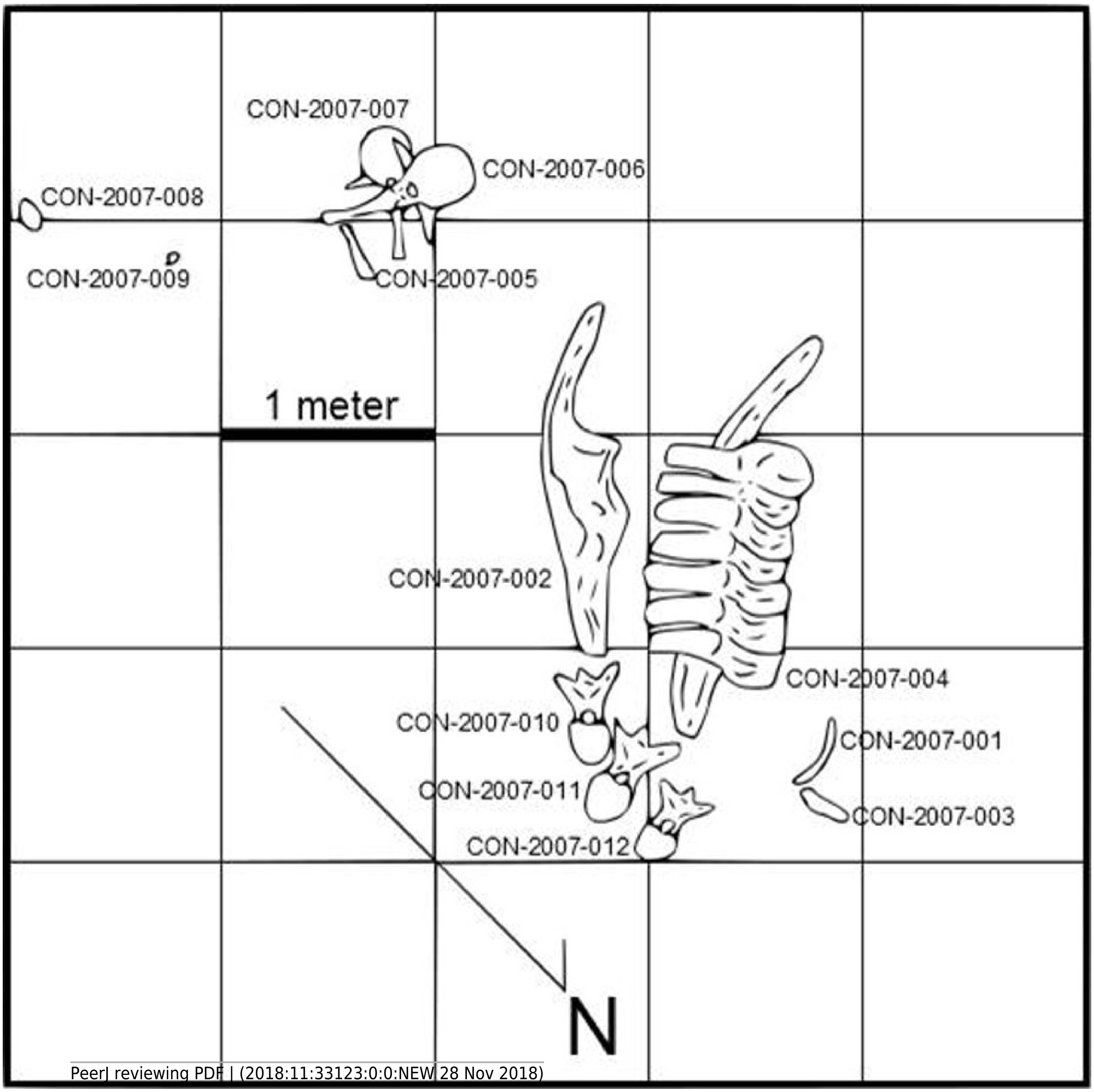

Figure 4

Punctured caudal vertebra of BMR P2007.4.1.

BMR P2007.4.1 in anterior (A) posterior (B) and ventral (C), including the two elliptical punctures on the ventral surface of the centrum (D, E).

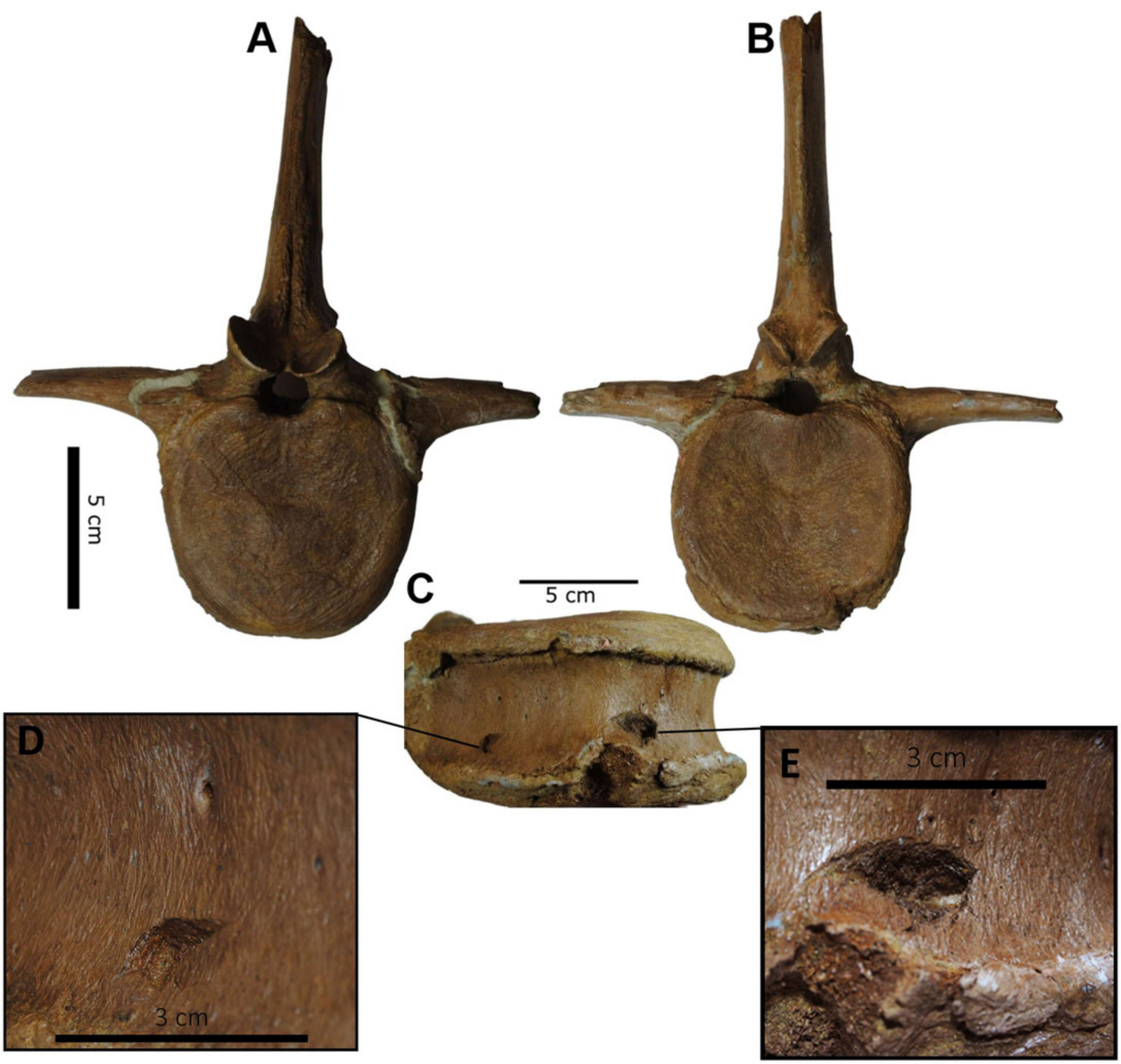

Figure 5

Silicone peel produced from BMR P2007.4.1.

Silicone peel produced from the ventral surface of the punctured caudal vertebra of BMR P2007.4.1 in vertical (A), and lateral (B) views. Note the traced outlines demonstrating the shape of the tooth casts.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

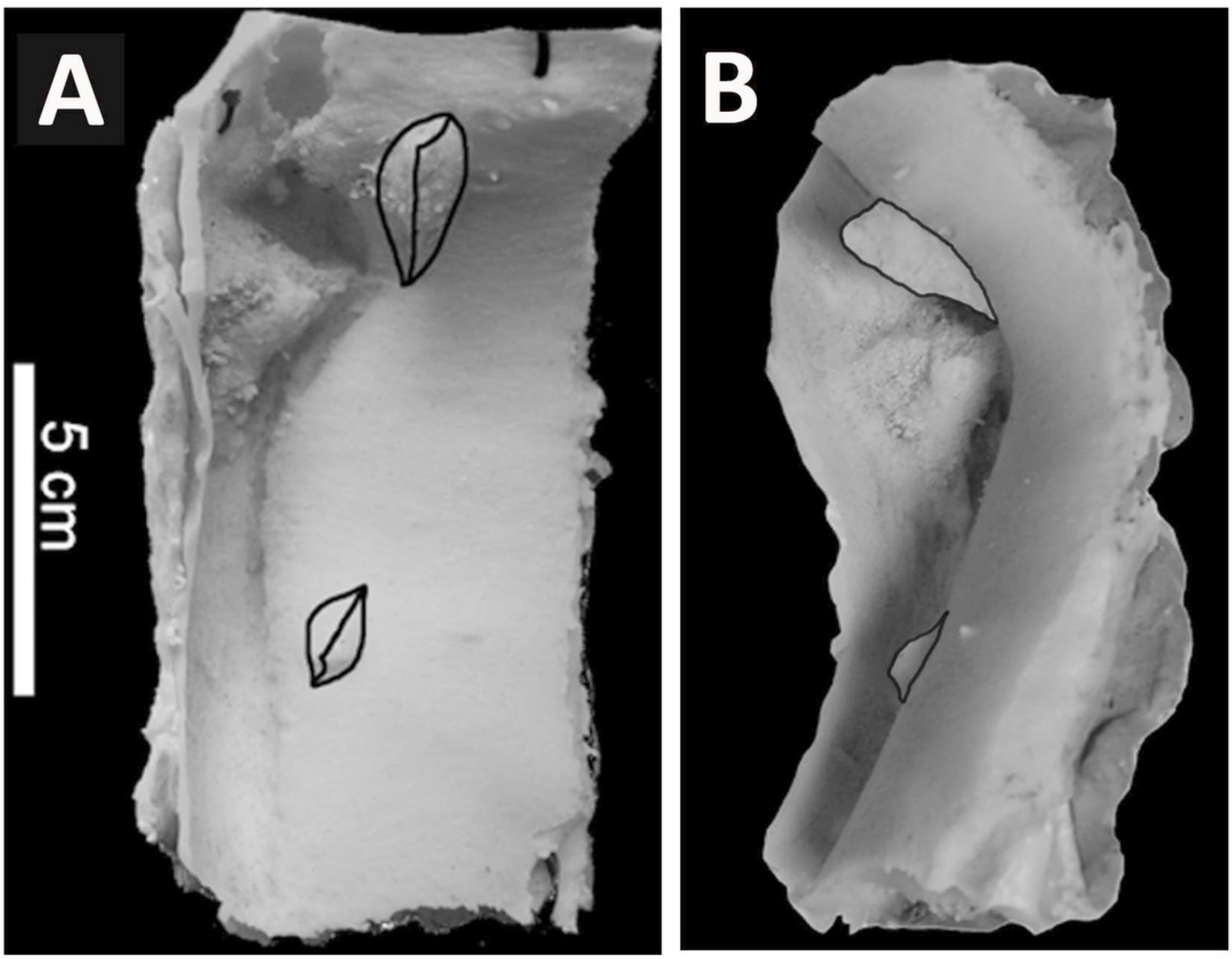

Figure 6

Casts of BMR P2002.4.1.

Casts of BMR P2002.4.1 maxilla (A) and dentary (B) to illustrate the tooth positions used for spacing measurements. Note the alternating replacement of teeth. Scale bars equal 10 cm.

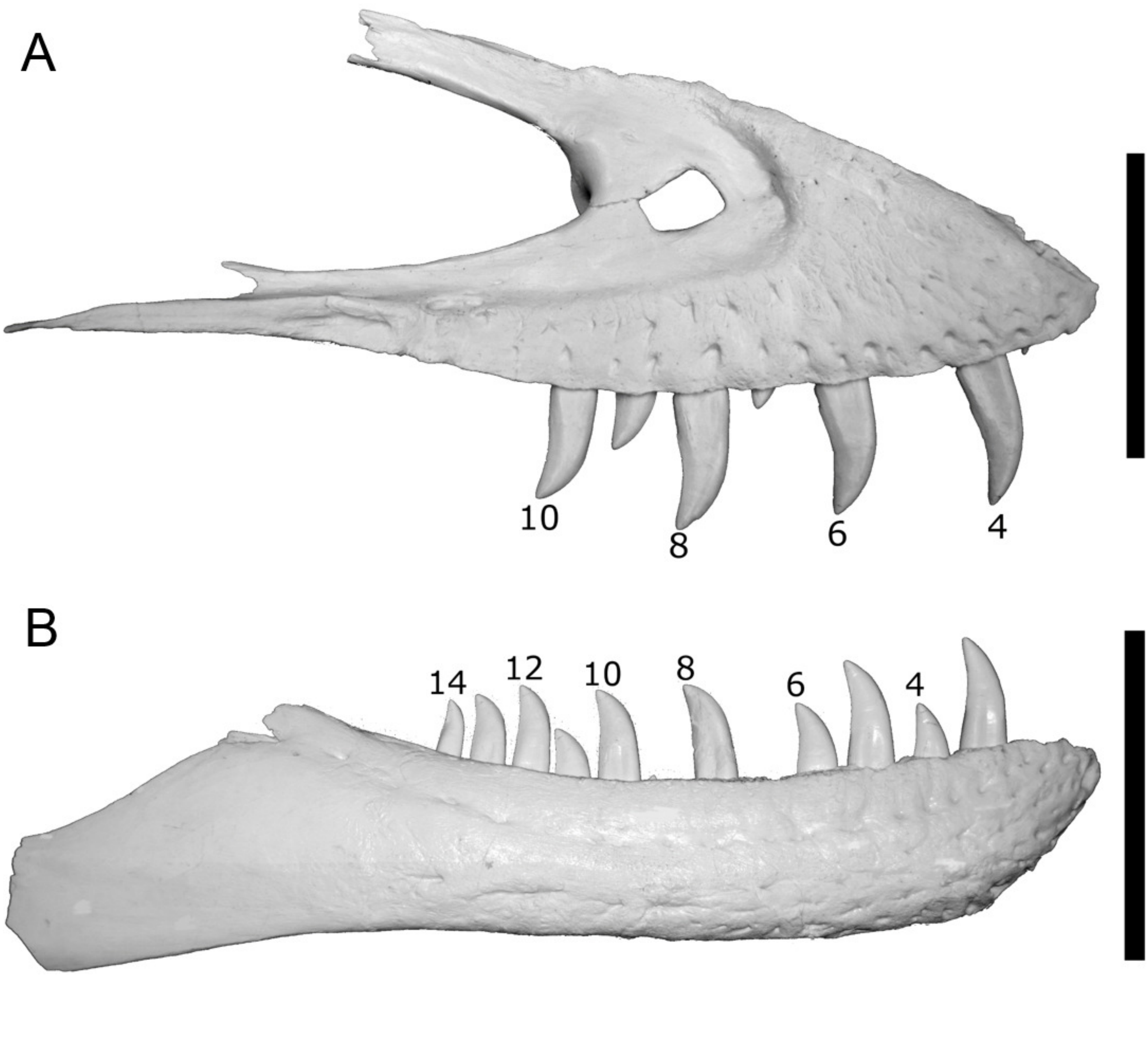

Figure 7

Maxillary and dentary measurements for BMRP 2002.4.1 and BHI 3033.

Maxillary and dentary measurements for BMRP 2002.4.1 and BHI 3033 mesiodistal and labiolingual dimensions at 5 mm depth compared to the bite marks on BMR P2007.4.1.

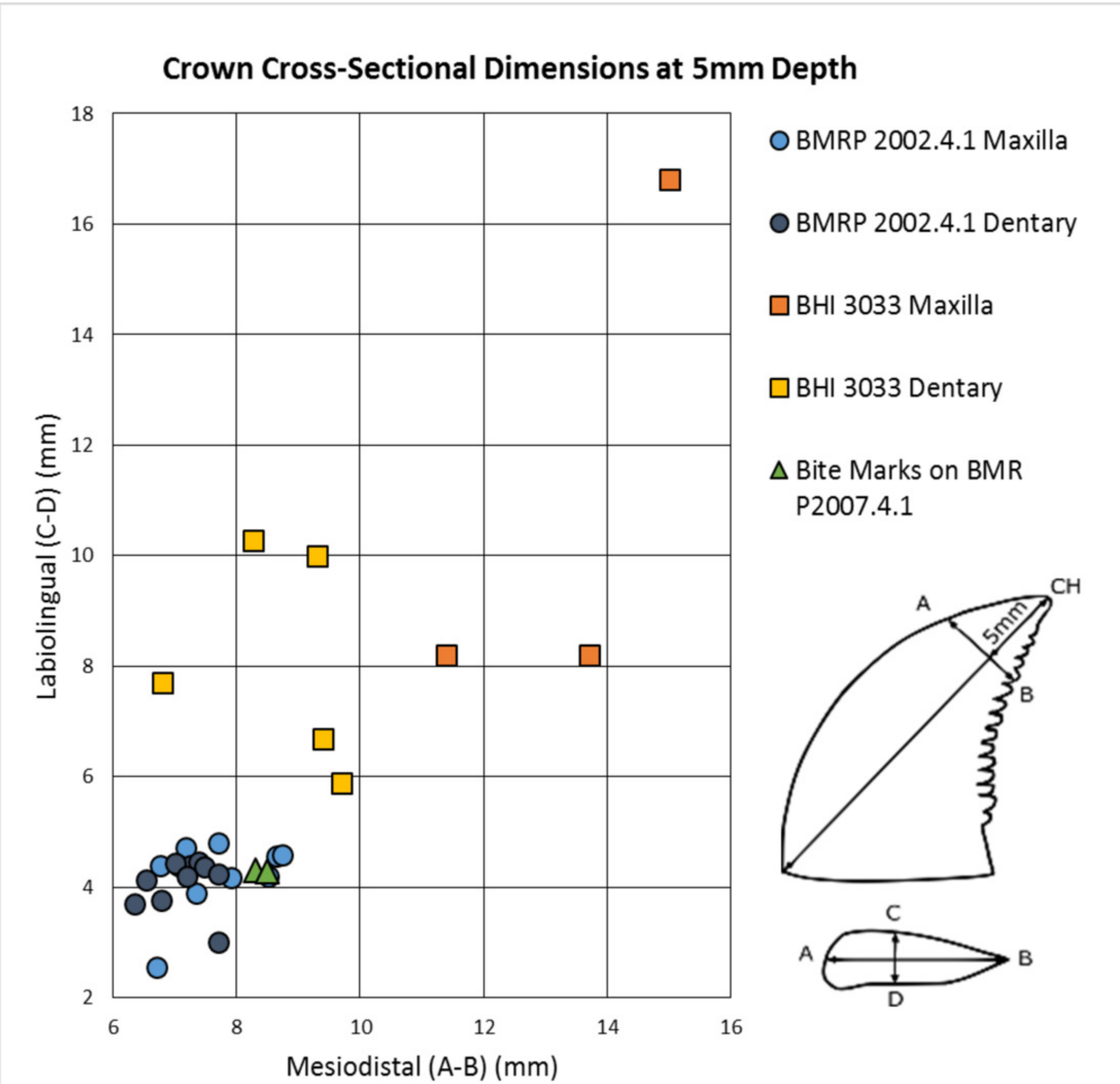

Figure 8

Digitized comparisons between tyrannosaur maxillae and BMR P2007.4.1.

Interactive manipulation of digitized NextEngine 3D scan of a cast of the right maxilla of BHI #3033 and BMR P2007.4.1 caudal vertebra.

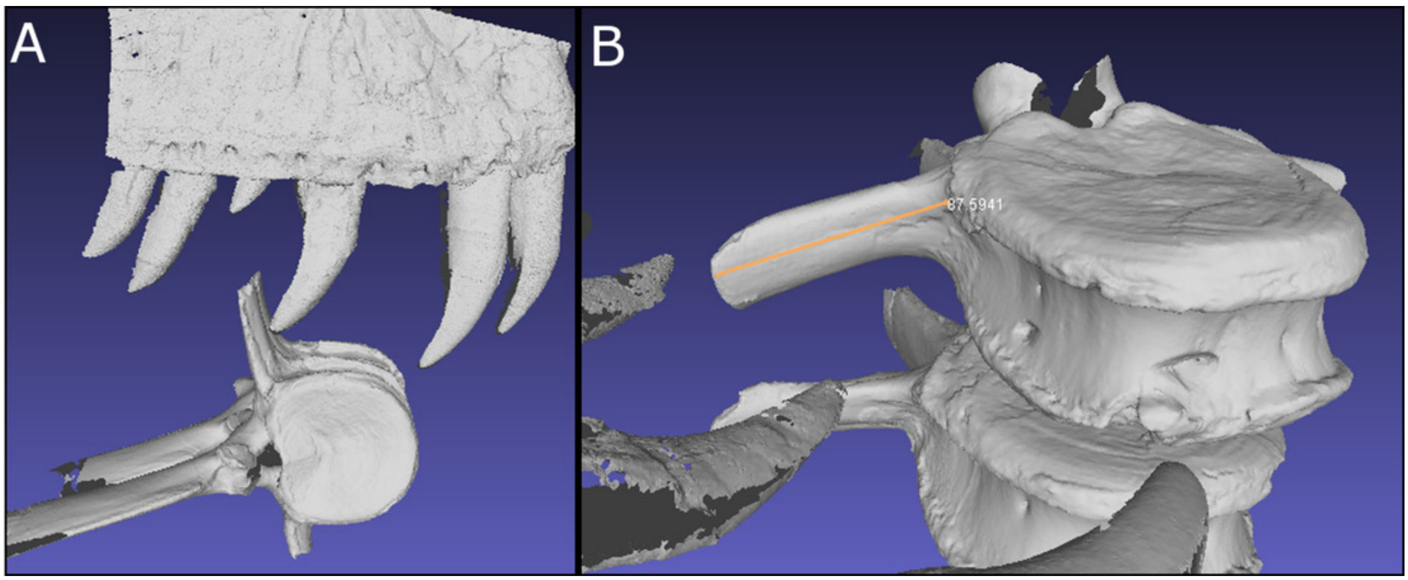

Figure 9

Digitized comparisons between BMR P2002.4.1 and BMR P2007.4.1.

Interactive manipulation of digitized NextEngine 3D scan of a cast of the right maxilla and dentary of BMR P2002.4.1, and BMR P2007.4.1 caudal vertebra.

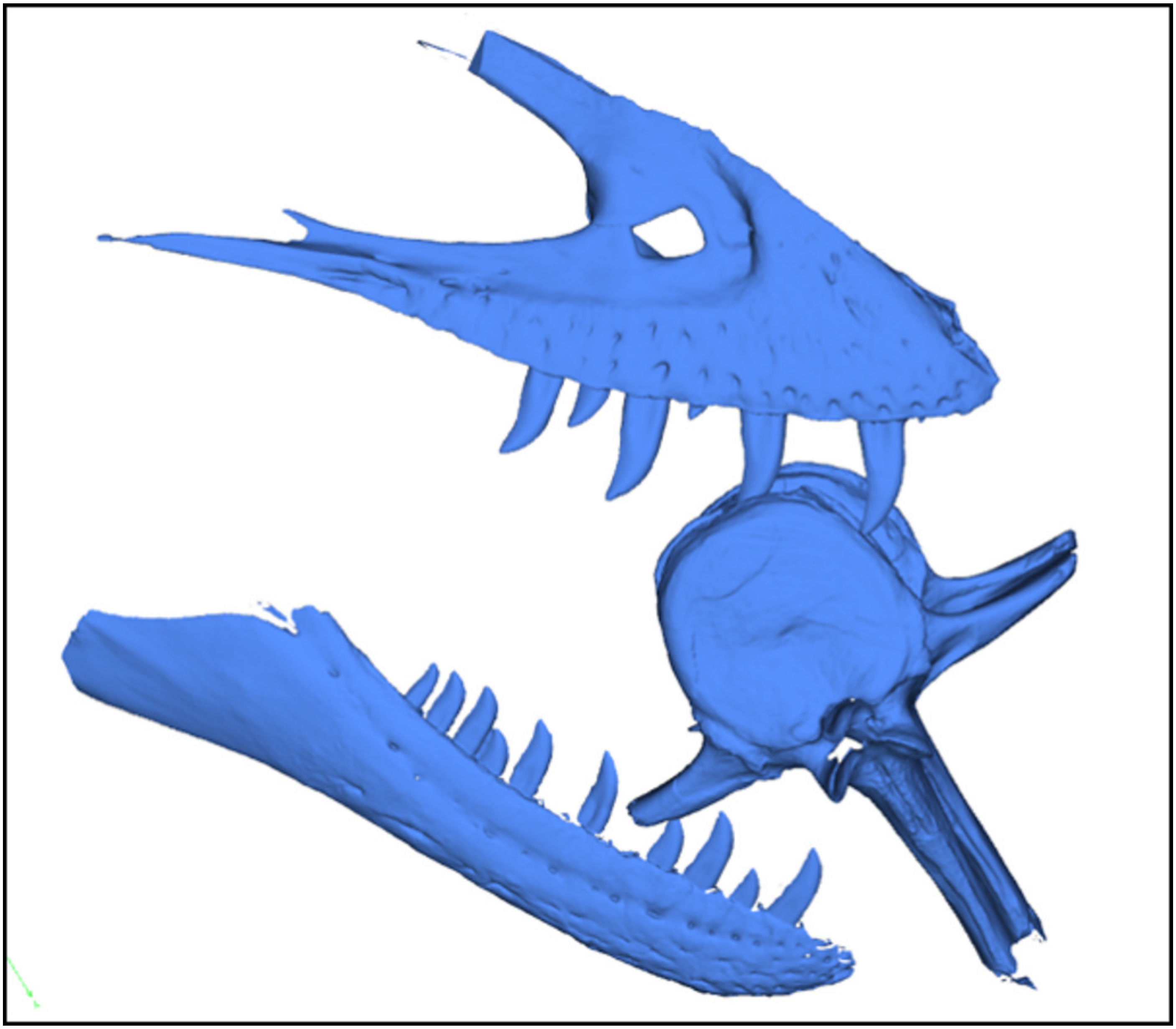

Table 1(on next page)

Skeletal elements from BMR P2007.4.1.

Recovered and recorded skeletal elements from the “Constantine Quarry” (BMR P2007.4.1) and taphonomic condition.

Field Number	**Element**	**State/Condition**
CON-2007-001	Rib fragment	Abraded
CON-2007-002	Left ilium	Heavily weathered
CON-2007-003	Rib fragment	Abraded
CON-2007-004	Sacrum and right ilium	Heavy to moderate weathering
CON-2007-005	Neural arch	Fractured, but mild weathering
CON-2007-006	Caudal vertebra	Mild weathering
CON-2007-007	Caudal vertebra	Mild weathering
CON-2007-008	Bone fragment	Heavily abraded
CON-2007-009	Shed *Saurornithoides sp.* tooth	No apparent abrasion
CON-2007-010	Dorsal vertebra	Heavily weathered, not collected
CON-2007-011	Dorsal vertebra	Heavily weathered, not collected
CON-2007-012	Dorsal vertebra	Heavily weathered, not collected

Table 2 (on next page)

Measurements of tooth crowns of tyrannosaur specimens.

Mesiodistal and labiolingual measurements of teeth at 5 mm depth from the crown apex for A) BHI 3033, B) BMR P2002.4.1, and C) the inferred bite marks on BMR P2007.4.1. All measurements are in mm.

A

BHI 3033	Maxilla		Dentary	
	Mesiodistal	Labiolingual	Mesiodistal	Labiolingual
	15	16.8	9.3	10.0
	11.4	8.2	8.27	10.27
	13.7	8.2	6.8	7.7
			9.4	6.7
			9.7	5.9

B

BMR P2002.4.1	Maxilla		Dentary	
	Mesiodistal	Labiolingual	Mesiodistal	Labiolingual
	6.77	4.4	7.06	4.39
	7.18	4.73	6.54	4.14
	7.35	3.9	6.78	3.77
	8.64	4.57	7.25	4.39
	7.91	4.19	7.39	4.47
	7.7	4.8	7.48	4.37
	8.74	4.59	7.0	4.44
	8.52	4.21	7.7	4.24
	6.71	2.56	7.19	4.2
			6.34	3.7
			7.7	3.01

C

BMR P2007.4.1 “Bite Marks”	Mesiodistal	Labiolingual
	8.3	4.31
	8.5	4.3

Table 3(on next page)

Measurements of crown spacing in tyrannosaur specimens.

Tooth crown spacing between maxillary (A) and dentary (B) teeth in the juvenile tyrannosaur BMR P2002.4.1. All measurements are in mm.

A

Crown Spacing	Maxillary (mm)
4-6	70.2
6-8	73.3
8-10	62.8
Average	68.7

B

Crown Spacing	Dentary(mm)
4-6	53.3
6-8	49.8
8-10	39.2
10-12	33.7
12-14	33
Average	41.8