Rare evidence for ‘gnawing-like’ behavior in a small-bodied theropod dinosaur (#57752)

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Rare evidence for ‘gnawing-like’ behavior in a small-bodied theropod dinosaur

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Mammalian predations show a higher degree of prey bone utilization relative to theropods dinosaurs, with this major ecological difference reflected in the frequency and morphology of tooth marks in modern and Cenozoic assemblage relative to Mesozoic ones. As such, prey bone utilization (i.e., gnawing, bone-breaking, osteophagy) may represent a key ecological strategy repeatedly exploited by mammalian carnivores but rarely in theropod dinosaurs. Here we described an isolated adult-sized hadrosaurid pedal ungual (III-4) from the Dinosaur Park Formation (Campanian) of southern Alberta which shows a unique pattern of bite marks from a small- to medium-sized theropod dinosaur. Thirteen distinct tooth marks occur in a restricted area of the ungual, and the pattern suggests up to six repeated, high-power bites delivered to the bone. The tracemaker cannot be definitively identified, but was likely a dromaeosaurid or very young tyrannosaurid. Tooth marks on at least four other Dinosaur Park Formation hadrosaur pedal unguals are reported, but the overall frequency of occurrence in unguals (< 1%) is much lower than that reported for other bones. The pattern of tooth marks on this specimen deviates from most described theropods tooth marks, and given the low volume of meat associated with the ungual, may represent theropod prey bone utilization as part of late-stage carcass consumption, and a behavior similar to mammalian gnawing.

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Abstract

Mammalian predations show a higher degree of prey bone utilization relative to theropod dinosaurs, with this major ecological difference reflected in the frequency and morphology of tooth marks in modern and Cenozoic assemblages relative to Mesozoic ones. As such, prey bone utilization (i.e., gnawing, bone-breaking, osteophagy) may represent a key ecological strategy repeatedly exploited by mammalian carnivores but rarely in theropod dinosaurs. Here we describe an isolated adult-sized hadrosaurid pedal ungual (III-4) from the Dinosaur Park Formation (Campanian) of southern Alberta which shows a unique pattern of bite marks from a small- to medium-sized theropod dinosaur. Thirteen distinct tooth marks occur in a restricted area of the ungual, and the pattern suggests up to six repeated, high-power bites delivered to the bone. The tracemaker cannot be definitively identified, but was likely a dromaeosaurid or very young tyrannosaurid. Tooth marks on at least four other Dinosaur Park Formation hadrosaur pedal unguals are reported, but the overall frequency of occurrence in unguals (< 1%) is much lower than that reported for other bones. The pattern of tooth marks on this specimen deviates from most described theropod tooth marks, and given the low volume of meat associated with the ungual, may represent theropod prey bone utilization as part of late-stage carcass consumption, and a behavior similar to mammalian gnawing.

Introduction

A major ecological and feeding behavior distinction between the Mesozoic theropod dinosaur and modern and Cenozoic mammalian predations is the difference in utilization of prey bones as a food source (Fiorillo 1991). Both modern and fossil carnivorous mammalian species have been shown to make extensive use of prey bones as a dietary source (Kruuk 1972; Haynes 1980; Van Valkenburgh 1996). This is often characterized by repeated, high-power bites to bone

extremities by premolars and molars, often for the purpose of exposing the lipid and nutrient rich marrow (Van Valkenburgh 1996; Van Valkenburgh 2007). This behavior may be considered 'gnawing', in that it follows the definition '*to bite or chew something repeatedly, usually making a hole in it or gradually destroying it'* (Cambridge 2016). This gnawing behavior is also often taxon and season specific, allowing for ecological inference based on gnawing damage (Haynes 1980; Haynes 1983). Indeed, bone-cracking is a specialized ecological strategy that has evolved several times within Carnivora (Van Valkenburgh 2007; Tseng 2013). While this gnawing behavior is most well-established in mammals, most commonly orders Carnivora and Rodentia, this behavior may be present in other taxa as well.

In contrast to the pattern in Recent and Cenozoic mammals, most research on Mesozoic theropod dinosaurs has suggested that prey bone utilization in theropods is limited, with little direct evidence in the way of gnawing behavior (Fiorillo 1991; Chure et al. 1998; Jacobsen 1998; Hone & Rauhut 2010). Patterns of tooth mark occurrence within Mesozoic assemblages support this interpretation in multiple ways. Firstly, relative to Recent and Cenozoic bone assemblages, there is a distinctly lower frequency of tooth marks in Mesozoic systems (Fiorillo 1991; Hone & Rauhut 2010). Additionally, these tooth-marked bone assemblages are dominated by scratch/scrape marks that do not penetrate the bone cortex, relative to puncture marks, suggesting these tooth-bone contacts are incidentally delivered while feeding on the surrounding soft tissue (Hone & Rauhut 2010). Finally, documented instances of theropod tooth marks can generally be characterized by a single bite, inflicting either scratches or punctures to the bone, but not repeated bites in a restricted area (Chure et al. 1998; Hone & Rauhut 2010). This suggests that prey bone utilization (i.e., gnawing, bone-breaking, osteophagy) is a key ecological strategy that was, and is, repeatedly exploited by mammalian carnivores, but not theropod dinosaurs (Hone & Rauhut 2010).

A possible exception of this pattern is in the Tyrannosauridae, where osteophagy may have been possible due to a combination of a strong bite and large, robust teeth (Hurum & Currie 2000; Hone & Rauhut 2010; Gignac & Erickson 2017). Despite this, direct evidence consistent with repeated biting on bones is rare (Erickson & Olson 1996; Hone & Watabe 2010; Dalman & Lucas 2021), with the isolated, raking, and likely incidental marks dominating the tyrannosaur toothmark record. Putative tyrannosaur coprolites have demonstrated a high volume of consumed bone on occasion (Chin et al. 1998; Chin et al. 2003), though this may be more consistent with ingestion of intact portions of smaller prey animals.

Here we report an isolated hadrosaurid pedal ungual that shows strong evidence for repeated, powerful, and localized biting behavior in a small to medium-sized theropod dinosaur. The pattern of tooth marks is inconsistent with incidental contact, and rather, is a rare case of gnawing or 'gnawing-like' behavior in theropod dinosaurs.

Materials & Methods

The specimen, Royal Tyrrell Museum of Palaeontology (TMP) 2018.012.0123, is an isolated hadrosaurid pedal ungual, collected from Bonebed 50 (specifically, Bonebed 50 east) in

the core area of Dinosaur Provincial Park, Alberta. The specimen was found as part of the Queen Mary University of London – Royal Tyrrell Museum of Palaeontology field school in 2018, and collected under Research and Collection Permit 18-510 (Alberta Tourism, Parks and Recreation) and permit to Excavate Palaeontological Resources 18-019 (Alberta Culture and Tourism).

Bonebed 50 is a mixed (macrofossil-microfossil) multitaxa bonebed in the lower to middle portion of the Dinosaur Park Formation, ~19 m above the contact with the underlying Oldman Formation. This site consists of a series of stacked palaeochannel sandstones, the basal lags of each hosting a high diversity and abundance of microvertebrate fossils, as well as disarticulated to partially articulated adult hadrosaur skeletons, including the type of *Corythosaurus excavatus* (Tanke & Russell 2012; Bramble et al. 2017), and isolated hatchling-to-nestling sized hadrosaur elements (Tanke & Brett-Surman 2001; Eberth & Evans 2011). Although at least three associated to articulated adult hadrosaur skeletons are known from this site, the ungual cannot be confidently associated with any of these, and likely represents an isolated specimen within the macrovertebrate component of the bonebed.

The ungual was almost completely encrusted with a soft to medium-hardness iron-rich siltstone. An airscribe on a low setting was gently used to remove most of this and a scalpel was used to remove the rest. The rock separated cleanly from the bone. An air abrasive on low air pressure and powder (sodium bicarbonate) flow settings was used as a final cleaning, followed by water and toothbrush. No adhesive, consolidant, or surface coat were applied.

Specimen photography was performed with a Canon EOS 6D (50 mm [1:1.4) and 24-105mm [1:4] lenses). Ammonium chloride power coating was used with photography to enhance the surface texture while homogenizing bone colour. Ammonium chloride was applied using the "dry method" *sensu* Parsley and colleagues (2018). All measurements were taken with digital calipers (150 cm) to the nearest tenth of a millimeter. Figures were prepared using Adobe Illustrator (V. 15.1.0) and Adobe Photoshop (V. 12.1). Statistical test were performed in the R programing language (Team 2009) using the functions *ks.test* (stats), and *chisq.test* (stats), while the histograms were created using the function *hist* (graphics), *lines* (graphics) and *density* (stats).

Results

Description - The specimen is complete, missing only abraded portions of the cortical bone along its extremities - largely the rim of the articular facet (Fig. 1A). It is unclear how much of this abrasion is recent as opposed to Cretaceous, but this may suggest limited transport of the specimen prior to deposition, or discovery. The ungual measures 105 mm in proximodistal length, 99 mm in maximum transverse width, and 49 mm it maximum height. The saddle shaped proximal articular face is 49 mm tall and 79 mm wide. The morphology and symmetry of the ungual indicates that it derives from digit three (i.e., III-4), the central and largest of the pedal digits, and the largest ungual (Fig. 2A). Given that the specimen is equivalent in size, or larger than, specimens regarded as adults of contemporaneous hadrosaurid species (i.e., *Gryposaurus*, *Corythosaurus*), it likely pertained to an adult-sized individual (Parks 1920).

A series of prominent tooth marks (observed in the field prior to collection) are present on the ventral (plantar) surface of the ungual, but no marks are seen on the dorsal or articular surface (Fig. 1A, B). A restricted area, ~30x20 mm, on one-half of the ventral surface adjacent to the articular facet bears 13 distinct tooth marks (Fig. 2B). The largest tooth mark is 10.5 mm long, and 3.3 mm wide, while the smallest is 2.7 mm long and 1.6 mm wide (Table 1). The majority of the tooth marks are approximately three times longer than wide, but the smallest are more equidimensional. The morphology of the tooth marks is somewhat intermediate between the elongate v-cross section furrows, and the circular to ovoid pits that have previously been described for theropod tooth marks (Erickson & Olson 1996; Jacobsen 1998). Although prominent, the marks are shallow, with the deepest marks around 1 mm in depth. The marks penetrate the smooth surface of the cortical bone, and expose the underling anteroposteriorly oriented fibers. Individual marks are numbered using Arabic numerals (Fig. 2C).

Relative to each other, the marks are not random in orientation or position. The long axes of all tooth marks are parallel, running ~20° to the transverse axis of the digit (Fig. 1A, 2B). Further, the marks are positioned in an approximate grid pattern, being aligned in two nearly perpendicular axes (Fig. 2C). The long axes of marks are nearly aligned with one of these grid axes (oriented distomedially) termed rows (labeled with Roman numerals), and lie nearly perpendicular to the other (oriented distolaterally) termed columns (labeled with lowercase letters) (Fig. 2C). All tooth marks with the exception of mark number 11 fit this discrete grid-like pattern. There are three columns (a-c) and at least four, but possible up to six rows (i-vi). Tooth mark spacing (based on midpoints) between successive marks within rows varies from 4.9 to 8.8 mm, with a mean of 7.0 mm, while spacing between successive marks in columns is smaller, from 4.0 to 7.4 mm with a mean of 5.3 mm (Table 2). The bone surface on which the marks are located is slightly convex in transverse curvature, with the proximodistal surface is strongly concave at the distolateral extreme.

Frequency of tooth marks on unguals - Despite the apparent oddity of bite marks to a hadrosaur ungual, TMP 2018.012.0123 is not an isolated occurrence. A second hadrosaur pedal ungual from the Dinosaur Park Formation, UALVP55092, appears to shows a cluster of three distinct tooth marks on the ventral (plantar) portion of the ungual, oriented at ~45° to the long axis of the ungual (Fig. 3A). In this second case, the marks appear to be a series of three parallel shallow furrows consistent with a single bite, and more in line with other described theropod feeding traces.

Given that two Dinosaur Park Formation hadrosaur unguals show unexpected bitemarks, a survey was undertaken to determine if this is a more common, but previously unrecognized, pattern. A total of 425 isolated hadrosaurid unguals (pedal and manual) from the Dinosaur Park and Oldman formations, were specifically examine for tooth marks (Supplemental Table S1). Only two cases of definitive tooth marks were found within this sample (Fig. 3B, C), suggesting the frequency of tooth marks on hadrosaur unguals is very low (< 1%). This is significantly lower than the reported frequency of tooth marks on both overall hadrosaurid bones, 14%

(47/339), and metapodials, 13% (16/120), from this formation (chi-square = 54.152 and 44.535, p = 1.856e-13 and 2.499e-11, respectively) (Jacobsen 1998).

These two other tooth marked unguals are smaller than TMP 2018.012.0123, and, as with UALVP55092, the marks are clusters of parallel (or nearly parallel) elongate furrows oriented at ~45° to the long axis of the ungual. The first of these specimens, TMP 1979.008.0769 (ungual II-3?), is 59 mm wide and 74 mm long, and preserves four tooth marks (11.0, 23.4, 25.1, and 10.9 mm in length) on the dorsolateral surface with intramark spacing of around 3.5 mm (Fig. 3B). The second specimen, TMP 1980.016.1215 (ungual III-4), is 59 mm wide and 64 mm long (est.), and also preserves four tooth marks (9.4, 7.5, 26.7, 8.1 mm in length) on the dorsal surface with intramark spacing of around 5.2 mm (Fig. 3C). In all four cases, marks are seen one on side of the ungual and not the other.

The frequency of tooth marks in non-ungual phalanges may be higher than for unguals, as several cases are known and have been reported for both hadrosaurid - TMP 1966.011.0022 (Jacobsen 1998), TMP 1981.023.0011 (Jacobsen 1998), TMP 1993.110.0003, TMP 2016.012.0096, TMP 2019.014.0004, UCMP 140601, (Erickson & Olson 1996) - and tyrannosaurid - UCMP 137538, MOR 1126 elements (Longrich et al. 2010). An allosaur pedal ungual with allosaur toothmarks has also been recently reported (Drumheller et al. 2020).

Discussion

Pattern of toothmarks - In total 13 distinct tooth marks are preserved, but their alignment in a grid-like pattern suggests these were the result of a combination of successive teeth in the toothrow making contact with the bone surface, and the tooth row moving laterally relative to the ungual between successive bites.

Given the alignment of the mark long axes, the relatively consistent within-row mark spacing, and the saddle shaped bone surface, it is likely that the rows (e.g., i, ii, iii etc.) represent individual bites, with successive teeth in the tooth row making aligned marks (Fig. 2C). The multiple rows represent the bone being moved laterally relative to the tooth row (or vice versa) between successive bites. The columns (e.g., a, b, c) therefore would be the same tooth making contact with the bone surface multiple times as the bone slid laterally relative to the tooth row between bites. Under this hypothesis there are up to three successive teeth in the tooth row that made contact with the bone, and a minimum of four, and possibly up to six, distinct bites. The relative equidistance between the successive bites (i.e., rows i-iv) indicates that the relative change in the position of the bone to the teeth differed by a consistent distance between each successive bite, ~5 mm. Under this hypothesis, the average distance between successive teeth is the toothrow is 7.0 mm. A slightly different hypothesis is illustrated if the long axes of the marks, rather than the position of the marks, are used as the primary alignments (Fig. 2D). Here lines illustrating possible tooth marks aligned in the toothrow are indicated. For this hypothesis, marks caused by successive teeth, and therefore the spacing between them, are less obvious to establish, but are roughly similar to that of the scenario above.

It is possible, though in our mind less likely, that the interpretation of these axes may be swapped. In this case, the columns (e.g., a, b, etc.) represent successive teeth in the toothrow making contact in a single bite, while the rows (e.g., i, ii, etc.) represent repositioning and lateral movement of the bone between successive bites. Under this hypothesis there are up to five successive teeth (with a potential one tooth gap) in the tooth row that make contact with the bone, and only three distinct bites. Under this hypothesis, the average distance between successive teeth in the toothrow is much smaller at 5.3 mm. Movement of the teeth across the bone surface during the bite in this hypothesis would be nearly orthogonal to the cross-sectional long axis of the tooth.

Several lines of evidence support the former interpretation relative to the later. The relative size and shape of the marks is more consistent within columns (e.g., marks 1, 4, 7) than within rows (e.g., marks 3, 4, 5). The spacing between successive marks is more consistent within rows, than within columns. The movement orthogonal to the cross-sectional long axis of the tooth would also increase the chance of tooth damage (see Hone & Chure 2018). Finally, the bone surface transected by the rows (i.e., i, ii) is gently convex, with the bites located at the high point of the transect. Conversely the bone surface transected by the columns (i.e., a, b) has a higher amplitude topography, is broadly concave, and bounded proximally and distally by bone surfaces that are above the level of the tooth marks, but that are not marked.

Regardless of which of these biting scenarios is correct, a series of closely spaced powerful bites were delivered to the ungual with the element repositioned relative to the tooth row between successive bites.

Tracemaker - The tracemaker responsible for the toothmarks can be narrowed down to a relatively small number of candidates. The various non-dinosaurian carnivores present in the Dinosaur Park Formation assemblage, including mammals, crocodylians and squamates, can be ruled out - see similar discussion in (Hone et al. 2018). Gnawing marks thought to derive from mammalian trace makers have been described from the Belly River Group, and these broadly resemble gnaw marks of modern rodents (Longrich & Ryan 2010). The bite marks of both modern and Cretaceous crocodylians leave characteristic deep, circular to sub-circular punctures (Njau & Blumenschine 2006; Noto et al. 2012; Boyd et al. 2013; Botfalvai et al. 2014; Drumheller & Brochu 2014) distinct from those seen on TMP 2018.012.0123. Finally, the tooth marks left by modern large squamates are dominated by thin arcing scours, with rare pits and no crushing observed (D'Amore & Blumenschine 2009).

Within Dinosauria, several clades of carnivorous (and potentially omnivorous) theropods represent potential tracemakers, including Tyrannosauridae, Dromaeosauridae, and Troodontidae. Of these potential tracemakers, Tyrannosauridae has the most comparative material for bite traces, both in terms of described material and absolute number of marks. Tooth marks thought to have been delivered by tyrannosaurs are dominated by v-shaped furrows and scours (both (sub)parallel and isolated), as well as distinct puncture-and-drag marks, punctures, and fine parallel striae resulting from denticle scrapes (Jacobsen 1995; Erickson & Olson 1996; Chin et

al. 1997; Jacobsen 1998; Fowler & Sullivan 2006; Hone & Watabe 2010; Bell et al. 2012; Rivera-Sylva et al. 2012; Robinson et al. 2016).

Dromaeosaurid tooth marks reported include those of *Saurornitholestes*, on the tibia a large azdarchid pterosaur (Currie & Jacobsen 1995), those of a velociraptorine, on *Protoceratops* bones (Hone et al. 2010), and those thought to pertain to *Deinonychus antirrhopus*, on the skeleton of *Tenontosaurus* (Gignac et al. 2010). In the former two cases the marks are shallow grooves or scours, while the latter case these are deeper V-shaped furrows. In addition to the scours and furrows, deeper, semi-circular 'bite and drag' marks are noted in by the velociraptorine (Hone et al. 2010), while deep punctures are described for *Deinonychus* (Gignac et al. 2010).

To our knowledge no suspected or definitive troodontid tooth marks have been described. Given their close relationship and general similarity to dromaeosaurs, they might however, have left similar traces if they bit into bones.

Given the lack of evidence of denticle spacing present on bite marks, and that both Tyrannosauridae and Dromaeosauridae were capable to delivering deep furrows and pits to the bone surface, the relative size and shape of the tooth marks, and the spacing between these marks may help do determine which is a more likely tracemaker. As noted by Hone and Chure (2018), drawing direct correlation between spacing of (presumed) serial tooth marks and tooth spacing in potential trace makers may be problematic. Factors such as curved bone surfaces, bite angle, and missing or misaligned teeth may add additional variation to the resultant tooth mark spacing and may make elimination of potential trace makers more challenging (Hone & Chure 2018). However, when a relatively consistent pattern of spacing between aligned tooth marks is observed, a most parsimonious first assumption in that this spacing is a least coarsely comparable to the spacing of teeth in the trace making individual. Comparisons between the spacing between the tooth marks on the ungual, and the potential theropod trace makers (see above) is shown in Fig. 4. The teeth (or alveoli) of the exemplar dentaries of the troodonid *Stenonychosaurus inequalis* average 2.7 or 3.4 mm apart, significant more closely spaced than the tooth marks in TMP 2018.012.0123 (Table 4, Fig. 4C, D).

For the two dromaeosaurid taxa, both *Saurornitholestes langstoni* and *Dromaeosaurus albertensis* are known from specimens that overlap the size range of the tooth marks on TMP 2018.012.0123. The *Saurornitholestes* dentary TMP 1988.121.0039 (mean spacing = 5.2 mm) is not statistically different from the within column tooth mark spacing (Table 4, Fig. 4E), while a larger specimen, TMP 1991.036.0112, (mean spacing = 7.6 mm) is not statistically different from the within row tooth mark spacing (Table 4, Fig. 4F). Similarly, the best specimen of *Dromaeosaurus,* AMNH 5356 (cast – TMP 1984.008.0001) shows spacing (mean = 7.7 mm) that is not statistically different from the within row tooth mark spacing (Table 4, Fig. 4G).

Relative to both Troodontidae and Dromaeosauridae, Tyrannosauridae is much better sampled from the Belly River Group, with a nearly complete ontogenetic series of jaws, missing only the smallest size classes. Given the small size and spacing the tooth marks only very small, immature, tyrannosaur individuals could represent potential trace makers. The two smallest

tyrannosaurid jaws from the Dinosaur Park Formation, the dentaries TMP 1990.081.0006 (mean spacing = 10.8) and TMP 1994.012.0155 (mean spacing = 12.0 mm), both show tooth spacing that is significantly greater than the spacing observed in TMP 2018.012.0123 (Table 4, Fig. 4H, I). While both these specimens are young juveniles (tooth row length of 2018.012.0123 = 165 mm) they do not represent the youngest/smallest extreme of tyrannosaurid ontogeny. It is possible that a younger/smaller tyrannosaur may have made the marks on TMP 2018.012.0123, but this would have to be a very immature individual smaller than that of any jaw currently known from the Belly River Group – with a tooth row length <165 mm.

Given these data it is not possible to confidently determine the taxonomy (or ontogeny) of the trace maker, but it can likely be narrowed down to either and adult-sized dromaeosaurid, or a very young tyrannosaurid. Regardless, these tooth marks suggest a potentially novel bone utilization, and may expand the evidence for bone utilization in Tyrannosauridae and/or Dromaeosauridae.

Behavioral hypotheses

Several possible behavior explanations may be put forward to explain the concurrence of such distinct tooth marks on the ungual.

Incidental contact while feeding - Regardless of whether the ungual was articulated with, or isolated from, the body, it would have had little meat in close association. While hadrosaur footprints indicated fleshy pads under the pedal phalanges (Langston Jr 1960; Currie et al. 1991), these would not have extended to the ungual, which would have largely been covered in a ketatinous hoof. While a keratinous hoof on the ungual would have had a very high protein content, keratin is resistant to vertebrate digestion, and was likely not a high value food item (Bragulla & Homberger 2009). Indeed, there are few bones in a hadrosaur skeleton that would be either less desirable for consumption, or further from areas of high consumption priority. Actualistic taphonomic studies of carcass utilization by modern mammalian carnivores consistently recover the phalanges and unguals as being bones with some of the lowest frequency of modification (Domínguez-Rodrigo 1999; Rodríguez-Hidalgo et al. 2013; Arilla et al. 2014; Rodríguez-Hidalgo et al. 2015; Arilla et al. 2019); these elements rank low in the carcass consumption sequence, and are largely used for their marrow (Blumenschine 1986; Marean et al. 1992). Additionally, the tooth marks on the bone surface of TMP 2018.012.0123 are not consistent with glancing contact between tooth and bone, but appear to be as a result of directly biting the bone surface. These tooth marks are not consistent with incidental marks during feeding, which appears to be the case for the majority of theropod tooth marks (Hone & Rauhut 2010).

Predation/Grasping – It is possible that the bites were delivered to the prey animal while it was still alive, and are the result of active predation. In this hypothesis, the predator may have grabbed on the hind foot of the hadrosaur with its jaws in an effort to slow down and, presumably with the combined effort of multiple individuals, bring down the prey. Multiple

bites, and repositioning of the tooth row between bites, may be indicative of the struggle between prey-and-predator.

There are several problems with this hypothesis. Firstly, the differential between potential predator and prey size is extreme. Mass estimates for adult-sized potential tracemakers range from 16 kg and 18 kg for *Dromaeosaurus albertensis* and *Saurornitholestes langstoni*, to 57 kg for *Troodon inequalis* (Campione et al. 2014; Benson et al. 2018). Mass estimates for an immature tyrannosaur are more challenging. Given scaling of the skull length to body mass (Therrien & Henderson 2007) in Theropoda, and femur to skull length in Tyrannosauridae (Currie 2003), and mass and femur length (Christiansen & Fariña 2004), the lower jaw of TMP 1994.012.0155 (29 cm long) would suggest a tyrannosaur tracemaker was no more than 32 or 44 kg, respectively. It should be noted that these estimation methods are not designed for immature individuals, are likely underestimates, and should be regarded as coarse at best. In comparison, adult-sized hadrosaurid taxa from Dinosaur Park Formation have mass estimates ranging from >3,000 to >5,000 kg (Campione & Evans 2012; Benson et al. 2018). This puts the mass of the hadrosaur at two orders of magnitude greater than the putative theropod tracemakers. This size differential is much great than that seen between predator and prey in analogue systems (Hone & Rauhut 2010). Given this size differential, it is difficult to believe that a theropod grabbing the rear ungual of a hadrosaur could not easily be kicked off. Further, if the multiple marks are interpreted as the result of a moving/struggling prey animal, one would expect there to be slippage and rotation of the marks, and the spacing and alignment of successive to be more irregular. Rather, the multiple bites are parallel and equidistant.

Play – Tyrannosaur tooth marks to isolated bones have been interpreted as evidence for play (Rothschild 2015). This hypothesis has been reviewed (Snively & Samman 2015), and it has been pointed out that it makes few testable predictions, and is difficult to falsify. Object based play behavior is within the behavioral extant phylogenetic bracket for Dinosauria (Snively & Samman 2015), so this behavior is theropod dinosaur may not be unexpected. Given its difficulty to test, however, this hypothesis is not addressed in detail here, though we suggest that the repeated nature of the bites at a single location on the ungual does not easily align with the idea of play.

Late-stage carcass consumption – Perhaps the most likely hypothesis is that the tooth marks are result of late-stage carcass consumption (Hone & Watabe 2010). Repeated, high powered bites delivered near the articular face of the ungual may have served to either sever or disarticulate the bone from the rest of the foot, or to break open the bone as part of a bone consumption strategy. The multiple parallel marks may also indicate repositioning of the bite to produce better leverage as the tracemaker attempted to pull apart the skeleton. The hypothesis of late-stage carcass consumption is consistent with interpretations of other densely tooth marked specimens attributable to tyrannosaurs (Erickson & Olson 1996; Fowler & Sullivan 2006; Hone & Watabe 2010).

This specimen, however, differs from these other reports in several major ways. First, the ungual is likely to have had little to no flesh in association, especially compared to a ceratopsian

pelvis (Erickson & Olson 1996; Fowler & Sullivan 2006) or hadrosaur humerus (Hone & Watabe 2010). As such this may represent an even more extreme example of late-stage carcass consumption than these previous reports. Second, although these other specimens show a high number of tooth marks, and are consistent with multiple bites to a single bone, these bites (with the possible exception of the deltopectoral crest of the humerus (Hone & Watabe 2010)) are not delivered to the same areas repeatedly. The marks to TMP 2018.012.0123 are restricted to a small area that was bitten up to six times. Third, previous records of bones with high density of tyrannosaurid bite-marks are attributable Tyrannosaurinae; i.e. *Daspletosaurus* (Fowler & Sullivan 2006), *Tarbosaurus* (Hone & Watabe 2010), and *Tyrannosaurus* (Erickson & Olson 1996). The tooth mark described here, may be attributable to either Albertosaurinae (i.e., *Gorgosaurus*) or Tyrannosaurinae (i.e., *Daspletosaurus*) or to Dromaeosauridae, broadening this behavior phylogenetically within Theropoda. Finally, these other reports document the activity in adult-size tyrannosaurs. If the bite marks described herein are from a tyrannosaur, they are from a very small, young individual, an individual at, or below, the size of the smallest known articulated skulls.

It is unclear if the purpose of the repeated, localized bites was to dismember the ungual from the rest of an articulated foot to expose articular cartilage or tendon, to break open the bone to expose the marrow, or for some other purpose.

We suggest that the general lower levels of bone exploitation by theropods may be linked to the difficulty of accessing the marrow cavity for them. Mammals may have proportionally larger marrow cavities than do dinosaurs (particularly ornithischians) for a given bone diameter, but in any case large dinosaurs will have absolutely thicker bone walls compared to mammals (e.g. sauropods and large ornithischians have absolutely larger femora than any living terrestrial mammals aside from perhaps elephants). Furthermore, large mammalian carnivores typically have more robust teeth for their size than do non-tyrannosaurid theropods, so overall would have a greater ability to process bone to obtain the marrow than most theropods, and thus the discrepancy in bone utilization between the two clades. The bones of dinosaurian juveniles or small taxa could still be broken and /or consumed and thus destroyed, but the lack of bite traces on large dinosaurian elements may at least in part reflect an inability to break into them.

Conclusions

A hadrosaurid pedal ungual bears a distinct pattern of tooth marks suggesting multiple, repeated, powerful bites delivered to a restricted area of the element. The morphology, size and spacing of the tooth marks suggest the tracemaker was a small-medium sized theropod dinosaur, likely a dromaeosaurid or young tyrannosaur. This behavior is most consistent with late-stage carcass consumption of an element that had limited association with the soft tissue considered to be the primary food source. Theropod bite marks on other hadrosaur unguals are known, but appear to occur at a very low frequency.

The traces left on these unguals are largely consistent with those left by gnawing behaviour. The mechanism of the bone processing behaviour is at least superficially similar to

gnawing in mammals, and may represent "gnawing-like" behavior. Indeed, if similar marks were left on a bone from a mammalian carnivore, "gnawing" would likely be considered an appropriate term. This specimen expands our understanding of prey bone utilization behavior in theropod dinosaurs, representing the strongest case for "gnawing-like" behavior in this clade. The occurrence of this prey bone utilization is also expanded, either phylogenetically into Dromaeosauridae, or ontogenetically into young tyrannosaurids.

Acknowledgements

TMP 2018.012.0123 was found by E. L. Clare, as part of the Queen Mary University of London – Royal Tyrrell Museum of Palaeontology field school in 2018. The authors thank Alberta Parks staff, specifically J. Blacklaws, for logistical support of this field school. UALVP 55092 was collected by C. Coy, and TMP 1979.008.0769 and TMP 1980.016.1215 were collected by J. Bahr and P. Currie respectively. Access to collections and specimen assistance was facilitated by T. Courtenay, H. Feeney, R. Russell, B. Sanchez and B. Strilisky (RTMP), and H. Gibbins, C. Coy and P. Currie (UALVP). D. Brinkman provided materials and assistance for ammonium chloride powder coating. I. Macdonald brought UALVP 55092 specimen to our attention, and provided the photograph. D. Evans, N. Gardner and F. Varriale provided useful discussion.

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Figure Captions:

Figure 1: Ammonium chloride coated photographs of the hadrosaurid pedal ungual TMP 2018.012.0123 showing bite marks (ventral/plantar view). (A) View of entire specimen, with marks highlighted in red (A'). (B) Close up of the bitten region, with marks highlighted in red and numbered in Arabic numerals (B'). All scale bars = 1 cm.

Figure 2: Position and orientation of bite mark on ungual and within hadrosaur pes. (A) Right articulated hadrosaurid pes in dorsal view, with in ungual of digit three highlighted (white) and the position of the tooth marks (ventral side) indicated in black – modified from (Prieto-Márquez 2014). (B) shaded line drawing of the ventral (plantar) view of the ungual TMP 2018.012.0123, showing the position of the bite marks (black). (C) Close up view of bite mark size, shape, and orientation, showing alignment of bites in rows (lowercase letter) and columns (Roman numerals) indicated by botted lines (based on Fig. 1B). (D) Close up view of bite marks showing potential alignment of tooth row parallel with tooth mark long axis. Hollow fills in C indicate potential bite marks missing from rows/columns. All scale bars = 1 cm.

Figure 3: Photographs (upper) and interpretive drawings (lower) of three isolated hadrosaurid pedal unguals with theropod toothmarks. (A) UALVP55092 in ventral (plantar) view, (B) TMP 1979.008.0769 in dorsal view, (C) TMP 1980.016.1215 in dorsal view. In lower drawings hatched areas indicate missing bone surface, dashed lines are approximate margins, and black indicates tooth marks. All specimens to same scale. Scale bar = 1 cm.

Figure 4. Size comparison of spacing between subsequent tooth marks on TMP 2018.012.0123 (A, B, J), and exemplars of potential theropod trace making taxa (C-I, K-N). (A-I) Histograms showing distributions on spacing between tooth marks (A, B) and teeth/alveoli (C-1): (A, B) TMP2018.012.0123, for rows (A) and column (B); (C, D) *Stenonychosaurus inequalis* – TMP 1967.014.0039, and 1982.016.0138; (E, F) *Saurornitholestes langstoni* – TMP 1988.121.0039 and 1991.036.0112; (G) *Dromaeosaurus albertensis* – TMP 1984.008.0001 (cast of AMNH 5356), and H, I) juvenile *Gorgosaurus libratus* – TMP 1990.081.0006 and 1994.012.0155. J-N) Scaled line drawings illustrating the morphology and size of the tooth traces exemplar dentaries (J) ungual TMP 2018.012.0123 in ventral view, with tooth marks shown in black; (K) medial view of reconstructed *Stenonychosaurus inequalis* (Troodontidae) dentary based on CMN 8540, redrawn from (Currie 1987); (L) medial view of complete dentary of *Saurornitholestes langstoni* (Dromaeosauridae) – based on TMP 1988.121.0039; (M) lateral view of complete dentary of *Dromaeosaurus albertensis* (Dromaeosauridae) – based on AMNH 5356, redrawn from (Currie

1995), (N) medial view of a dentary of a juvenile *Gorgosaurus libratus* (Tyrannosauridae) - based on TMP 1994.012.0155. Lines above dentaries indicates tooth size/alveolar spacing. All specimens to same scale. Scale bar = 1 cm.

Table 1: Linear measurements of the 13 tooth marks on TMP 2018.012.0123. See Fig. 1B for mark numbers.

Table 2: Spacing between successive tooth marks by both row (i, ii, etc.) and column (a, b, etc.) on TMP 2018.012.0123, see Fig. 2C.

Table 3: Spacing between successive tooth positions (or alveoli) in tooth rows across specimens of several potential tracemakers

Table 4: Results of Kolmogorov-Smirnov test (two sample), comparing the spacing between successive tooth positions (or alveoli) in TMP 2018.012.0123 with specimens of several potential tracemakers.

Figure 1

Ammonium chloride coated photographs of the hadrosaurid pedal ungual TMP 2018.012.0123 showing bite marks (ventral/plantar view).

(A) View of entire specimen, with marks highlighted in red (A'). (B) Close up of the bitten region, with marks highlighted in red and numbered in Arabic numerals (B'). All scale bars = 1 cm.

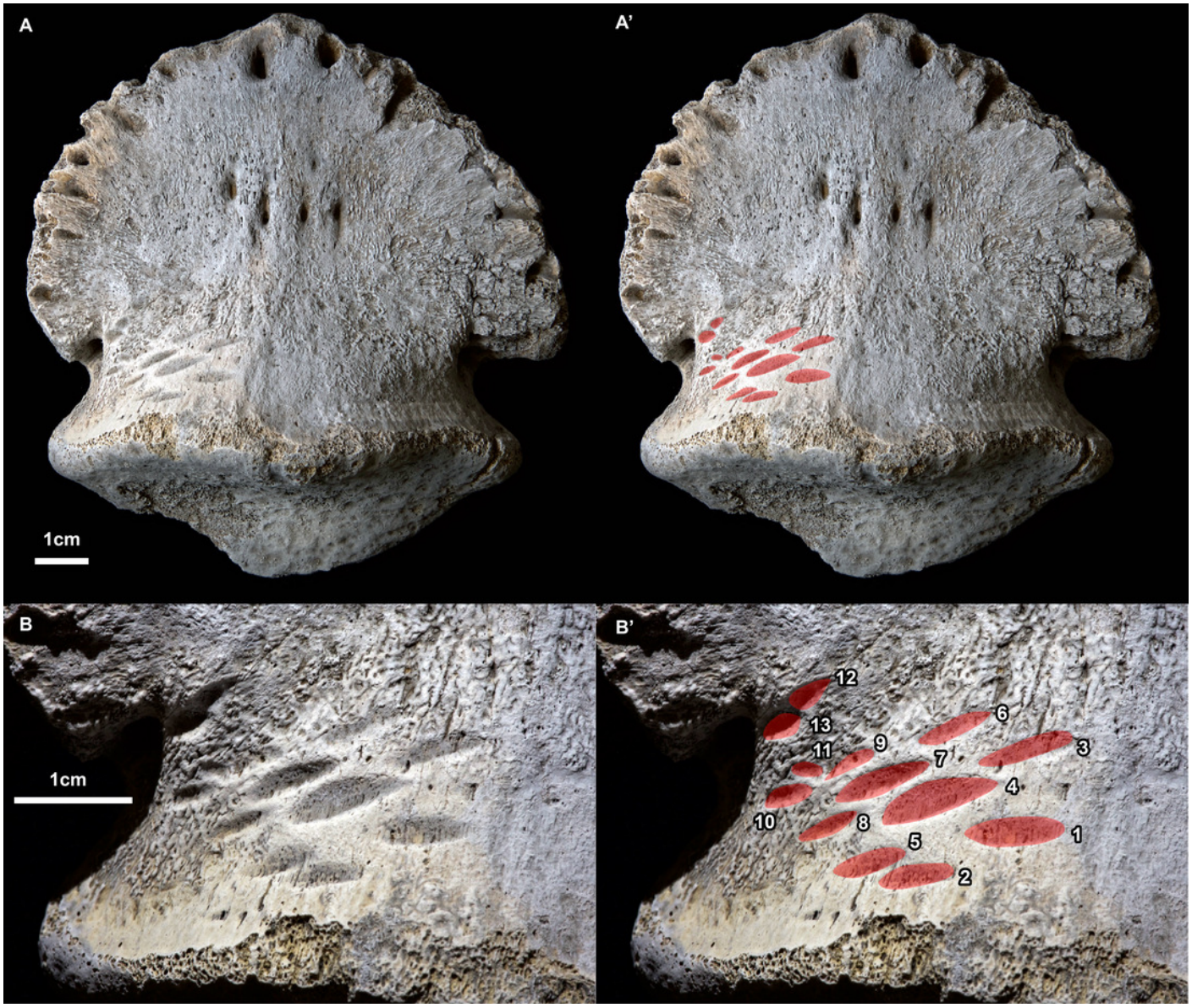

Figure 2

Position and orientation of bite marks on ungual and within hadrosaur pes.

(A) Right articulated hadrosaurid pes in dorsal view, with in ungual of digit three highlighted (white) and the position of the tooth marks (ventral side) indicated in black – modified from (Prieto-Márquez 2014) . (B) shaded line drawing of the ventral (plantar) view of the ungual TMP 2018.012.0123, showing the position of the bite marks (black). (C) Close up view of bite mark size, shape, and orientation, showing alignment of bites in rows (lowercase letter) and columns (Roman numerals) indicated by dotted lines (based on Fig. 1B). (D) Close up view of bite marks showing potential alignment of tooth row parallel with tooth mark long axis. Hollow fills in C indicate potential bite marks missing from rows/columns. All scale bars = 1 cm.

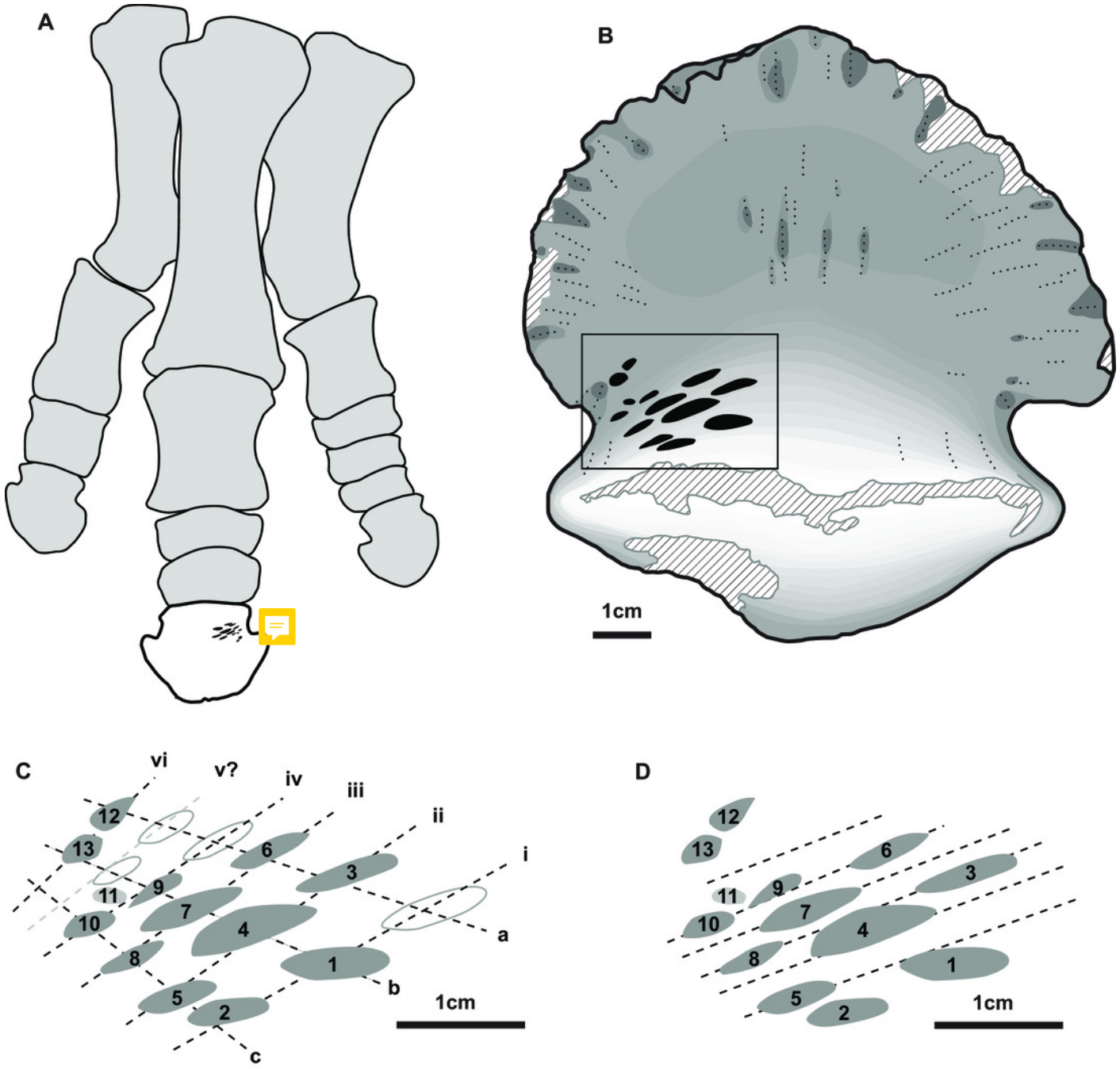
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Figure 3

Photographs (upper) and interpretive drawings (lower) of three isolated hadrosaurid pedal unguals with theropod toothmarks.

(A) UALVP55092 in ventral (plantar) view, (B) TMP 1979.008.0769 in dorsal view, (C) TMP 1980.016.1215 in dorsal view. In lower drawings hatched areas indicate missing bone surface, dashed lines are approximate margins, and black indicates tooth marks. All specimens to same scale. Scale bar = 1 cm.

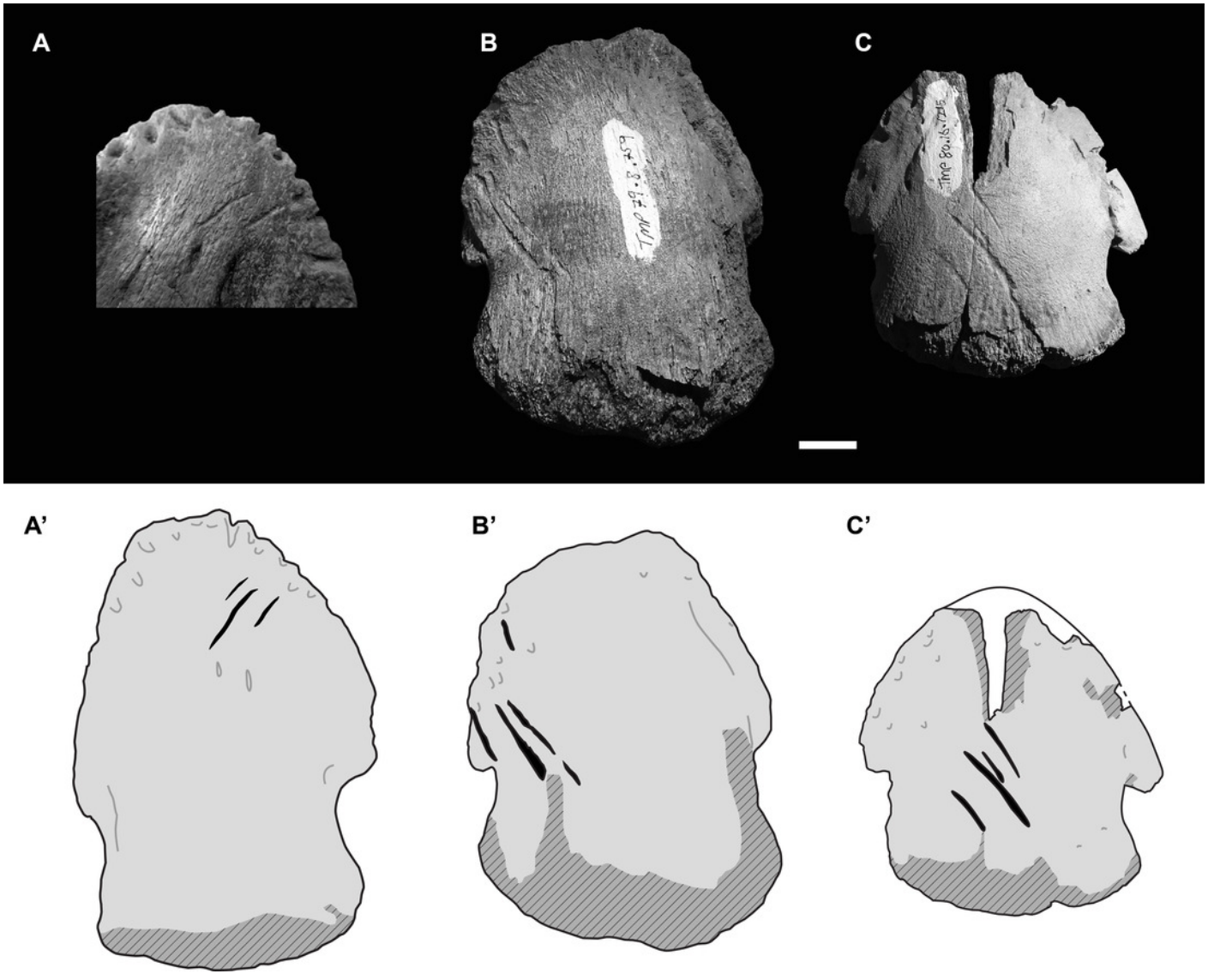
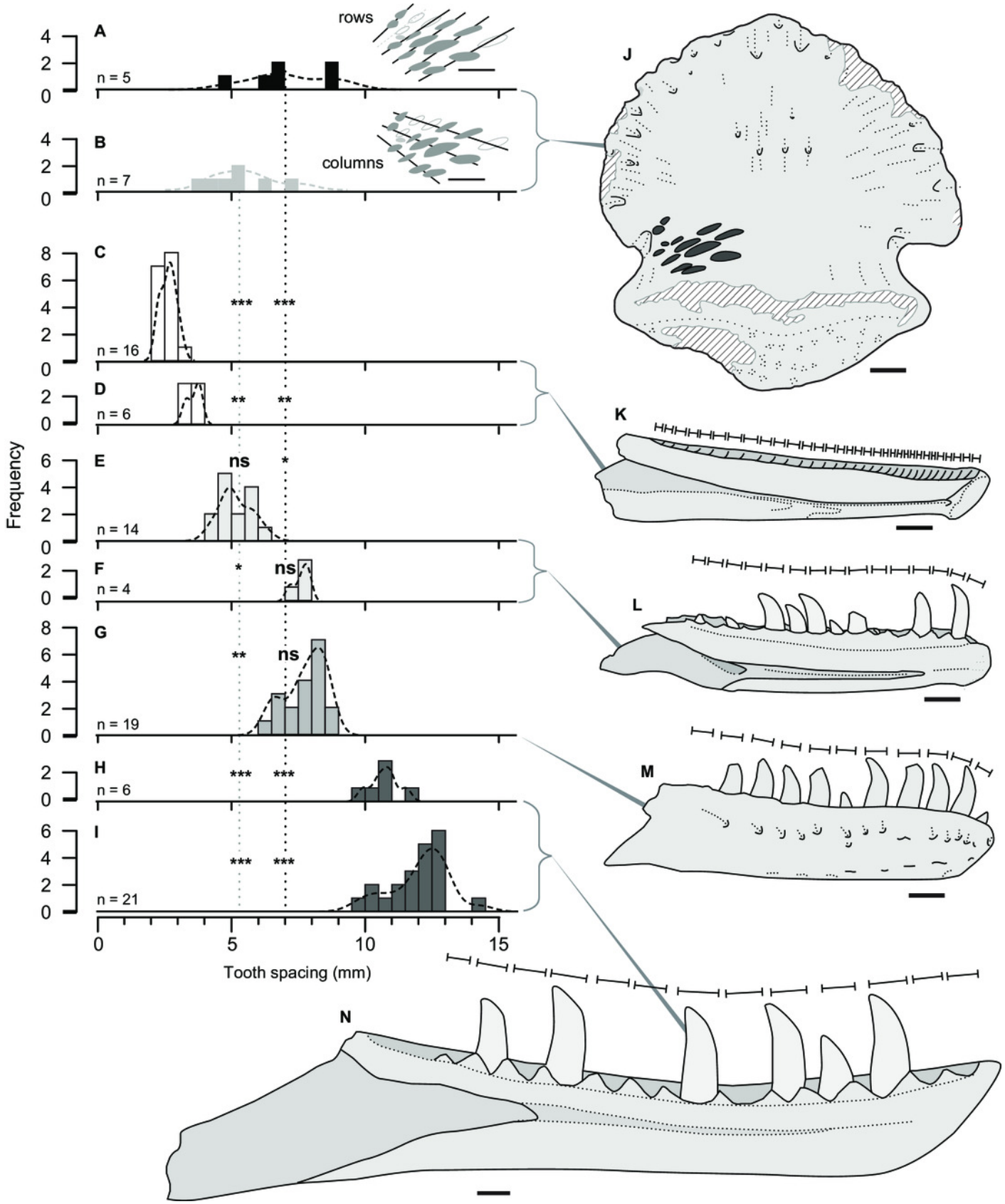


Figure 4

Size comparison of spacing between subsequent tooth marks on TMP 2018.012.0123 (A, B, J), and exemplars of potential theropod trace making taxa (C-I, K-N).

(A-I) Histograms showing distributions on spacing between tooth marks (A, B) and teeth/alveoli (C-I): (A, B) TMP2018.012.0123, for rows (A) and column (B); (C, D) *Stenonychosaurus inequalis* – TMP 1967.014.0039, and 1982.016.0138; (E, F) *Saurornitholestes langstoni* – TMP 1988.121.0039 and 1991.036.0112; (G) *Dromaeosaurus albertensis* – TMP 1984.008.0001 (cast of AMNH 5356), and H, I) juvenile *Gorgosaurus libratus* – TMP 1990.081.0006 and 1994.012.0155. J-N) Scaled line drawings illustrating the morphology and size of the tooth traces exemplar dentaries (J) ungual TMP 2018.012.0123 in ventral view, with tooth marks shown in black; (K) medial view of reconstructed *Stenonychosaurus inequalis* (Troodontidae) dentary based on CMN 8540, redrawn from (Currie 1987) ; (L) medial view of complete dentary of *Saurornitholestes langstoni* (Dromaeosauridae) – based on TMP 1988.121.0039; (M) lateral view of complete dentary of *Dromaeosaurus albertensis* (Dromaeosauridae) – based on AMNH 5356, redrawn from (Currie 1995) , (N) medial view of a dentary of a juvenile *Gorgosaurus libratus* (Tyrannosauridae) - based on TMP 1994.012.0155. Lines above dentaries indicates tooth size/alveolar spacing. All specimens to same scale. Scale bar = 1 cm.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Frequency
Tooth spacing (mm)
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Table 1(on next page)

Linear measurements of the 13 tooth marks on TMP 2018.012.0123.

See Fig. 1B for mark numbers.

Table 1: Linear measurements (longest axis) of the 13 tooth marks on TMP 2018.012.0123. See Figure 1B for mark numbers.

Mark	Row	Column	Length (mm)	Width (mm)
1	i	b	7.8	2.7
2	i	c	6.5	2.1
3	ii	a	7.9	2.4
4	ii	b	10.5	3.3
5	ii	c	6.6	2.3
6	iii	a	7.8	2.1
7	iii	b	8.5	2.3
8	iii	c	4.7	1.6
9	iv	b	5.8	1.8
10	iv	c	5.1	1.6
11	v?	c?	2.7	1.6
12	vi	a?	5.0	2.3
13	vi	b?	4.0	2.3
Mean			6.4	2.2

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Table 2(on next page)

Spacing between successive tooth marks by both row (i, ii, etc.) and column (a, b, etc.) on TMP 2018.012.0123.

See Fig. 2C for row and column designation.

Table 2: Spacing between successive tooth marks by both rows (i, ii, etc.) and columns (a, b, etc.) on TMP 2018.012.0123, see Figure 2C.

Alignment	Marks	Distance (mm)
Rows		
i	1, 2	8.8
ii	3, 4	8.6
ii	4, 5	6.8
iii	6, 7	6.6
iii	7, 8	4.9
iv	9, 10	6.4
	Mean	**7.0**
Columns		
a	3, 6	6.1
b	1, 4	7.4
b	4, 7	4.9
b	7, 9	4.2
c	2, 5	4.0
c	5, 8	5.5
c	8, 10	5.2
	Mean	**5.3**

Table 3(on next page)

Spacing between successive tooth positions (or alveoli) in tooth rows across specimens of several potential tracemakers.

Table 3: Spacing between successive tooth positions (or alveoli) in tooth rows across specimens of several potential tracemakers.

Taxon	Specimen	Element																	Mean (mm)	Count (n)
Gorgosaurus libratus - juv.	TMP 1994.012.0155	R. Dent.	12.6	12.3	12.9	12.8	11.9	12.8	12.1	12.4	12.7	10.3	9.6						12.0	**11**
Gorgosaurus libratus - juv.	TMP 1994.012.0155	L. Dent.	11.4	12.5	14.2	12	12.9	12	12.1	11.2	10.7	10.1							11.9	**10**
Gorgosaurus libratus - juv.	TMP 1990.081.0006	R. Dent.	10.7	10.5	11	11.6	11	10											10.8	**6**
Saurornitholestes langstoni	TMP 1988.121.0039	L. Dent.	5.8	4.9	5	5.6	6.4	5.1	5.2	4.9	5	5.9	5.9	4.9	4.3	4.4			5.2	**14**
Saurornitholestes langstoni	TMP 1991.036.0112	L. Dent.	7.2	7.6	7.9	7.8													7.6	**4**
Stenonychosaurus inequalis	TMP 1967.014.0039	L. Dent.	2.2	2.2	2.1	2.6	2.7	2.5	2.6	2.5	2.6	2.3	2.8	2.7	2.3	2.9	2.9	3.1	2.6	**16**
Stenonychosaurus inequalis	TMP 1982.016.0138	L. Dent.	3.6	3.6	3.6	3.1	3.4	3.1											3.4	**6**
Dromaeosaurus albertensis	TMP 1984.008.0001	L. Dent.	6.3	8.3	8.2	8.1	7.9	7.8	7.3	7.6	8.5								7.8	**9**
Dromaeosaurus albertensis	TMP 1984.008.0001	R. Dent.	6.7	6.6	8.3	8.5	8.7	8.6	8.2	7.6	7.4	6.6							7.7	**10**

Table 4(on next page)

Results of Kolmogorov-Smirnov test (two sample), comparing the spacing between successive tooth positions (or alveoli) in TMP 2018.012.0123 with specimens of several potential tracemakers.

Table 4: Results of Kolmogorov-Smirnov test (two sample), comparing the spacing between successive tooth positions (or alveoli) in TMP 2018.012.0123 with specimens of several potential tracemakers.

			Toothmark Spacing	
Potential Tracemakers Tooth Spacing			Rows	Columns
Specimen	Taxon	N	6	7
TMP 1967.014.0039	*Stenonychosaurus inequalis*	21	**0.0003242**	**0.0001179**
TMP 1982.016.0138	*Stenonychosaurus inequalis*	6	**0.004958**	**0.003125**
TMP 1988.121.0039	*Saurornitholestes langstoni*	14	**0.01525**	0.8407
TMP 1991.036.0112	*Saurornitholestes langstoni*	4	0.181	0.0303
TMP 1984.008.0001	*Dromaeosaurus albertensis*	16	0.2989	**0.001088**
TMP 1990.081.0006	*Gorgosaurus libratus* - Juvenile	6	**0.004958**	**0.003125**
TMP 1994.012.0155	*Gorgosaurus libratus* - Juvenile	19	**0.0001769**	**5.51E-05**