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New information on scavenging and selective feeding behaviour of tyrannosaurids

DAVID W.E. HONE and MAHITO WATABE



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Feeding traces for carnivorous theropod dinosaurs are typically rare but can provide important evidence of prey choice and mode of feeding. Here we report a humerus of the hadrosaurine *Saurolophus* which was heavily damaged from feeding attributed to the giant tyrannosaurine *Tarbosaurus.* The bone shows multiple bites made in three distinctive styles termed "punctures", "drag marks" and "bite-and-drag marks". The distribution of these bites suggest that the animal was actively selecting which biting style to use based on which part of the bone was being engaged. The lack of damage to the rest of the otherwise complete and articulated hadrosaur strongly implies that this was a scavenging event, the first reported for a tyrannosaurid, and not feeding at a kill site.

Key words: Dinosauria, Theropoda, *Tarbosaurus*, palaeoecology, carnivory, predation, scavenging.

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Introduction

Feeding traces in the fossil record can potentially tell us much about the habits of the carnivores that leave those traces behind (Erickson and Olson 1996; Carpenter 2000; Hone and Rauhut 2010; Hone et al. 2010). In the case of dinosaurian palaeontology, they are the most likely kind of ichnite to provide information on predator-prey relationships given the rarity of stomach contents, and the very great difficulty of determining if two sets of footprints of putative predator and prey species were laid down in conjunction with a trophic interaction. Nevertheless feeding traces remain relatively rare (Fiorillo 1991) and each new one can potentially provide important information about prey choice, feeding style and predation and/or scavenging depending on the available information.

Records of dinosaur feeding traces are mixed, with some specific examples being described in detail (e.g., Currie and Jacobsen 1995; Hone et al. 2010) and others simply registered as a part of a catalogue of bite marks on many specimens (e.g., Hunt et al. 1994; Jacobsen 1998). One well-described specimen that records predator-prey interaction consists of multiple bite marks on a *Triceratops* pelvis attributed to *Tyrannosaurus*. The feeding traces demonstrate the biting patterns and bite forces of a large tyrannosaurid (Erickson and Olson 1996; Erickson et al. 1996), which left deep puncture marks on the bone and bit through part of the ilium. This case is unusual in the number of marks and the extent of the damage on the pelvis, but in another sense it is a typical theropod feeding trace as only one kind of bite mark dominates. Other bite traces show a similar pattern of either light scrape marks (the tooth moving across the surface of the bone e.g., Jacobsen 1998; Chure et al. 2000) or puncture marks (e.g., Buffetaut et al. 2004; Fowler and Sullivan 2006) but little evidence of both (though see below). One possible exception of this pattern is seen where a velociraptorine tooth lies wedged into a bone but is surrounded by only drag marks (Currie and Jacobsen 1995), though this tooth may have become lodged in the bone from an attempted scrape as opposed to a bite.

Here we document a definitive case of multiple feeding styles being applied to a single bone, a *Saurolophus* humerus that was damaged by feeding from a large tyrannosaurid, most likely *Tarbosaurus*. The specimen exhibits three distinct kinds of bite traces on different parts of the bone and provides evidence not only of a theropod using different feeding styles, but of actively selecting a feeding style appropriate to the target area of bone.

Institutional abbreviations.—HMNS, Hayashibara Museum of Natural Sciences, Okayama, Japan; MPC, Mongolian Palaeontological Center, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia.

Geological setting

A near complete skeleton of the genus *Saurolophus* (Ornithopoda: Hadrosauridae) was excavated from a fluvial sandstone

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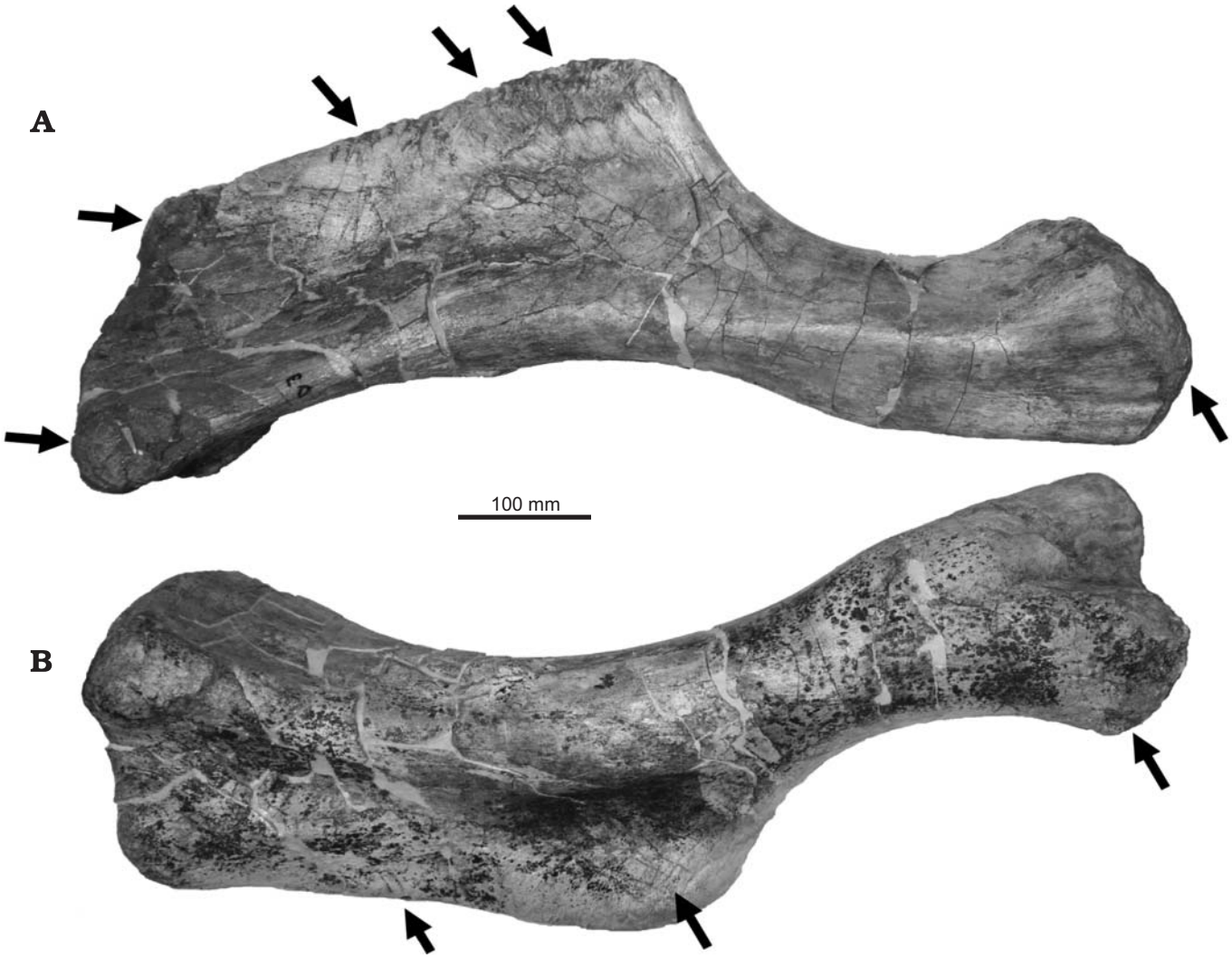


Fig. 1. MPC-D100/764, a left humerus of hadrosaurid *Saurolophus* from the Maastrichtian Bugin Tsav locality in Mongolia, in medial (**A**) and lateral (**B**) views (proximal end to the left and distal to the right) with major areas of bite marks indicated by the black arrows.

layer in 1995 by the HMNS-MPC joint paleontological expedition party. The specimen was collected from Bugin Tsav (part of the Maastrichtian Nemegt Formation), located in the northeastern rim of Ingeni Khovur Basin, in the western area of the Gobi Desert. The sandstone layer including the skeleton contains rich rip-up-clusts of underlying mudstone layers (overbank deposits). GPS coordinates were taken as N43° 51'23" E100° 01'08" at the site, at an altitude of 950 m. Based on trough cross stratification in a hard sandstone layer overlying the skeleton, the direction of the palaeocurrent runs parallel to the cranio-caudal axis of the skeleton.

Description

The specimen of *Saurolophus* is largely complete and articulated and of exceptionally good quality (MPC-D100/764, currently on loan at HMNS). This specimen is being described in full by other authors and will not be discussed in detail here. The specimen was an adult animal (both the skull bones and neurocentral arches of the vertebrae are fused) approximately 12 m in length, and is missing the very distal end of the tail, some centra of the dorsal vertebrae (thought not the neural arches), part of the lower jaw and most of the forelimbs. Of the forelimbs, only the right scapula and the left humerus remain. This is important as all of the observable damage through feeding is to this left humerus and no other traces can be observed on any other part of the specimen. One possible single bite mark is present on one tibia, but this is more likely to be a muscle attachment scar, a concept reinforced by the lack of any other traces on the bone. There are several very small pathologies on the proximal and mid caudals of the *Saurolophus* specimen, but none appear to be the result of healed bite wounds (cf. Carpenter 2000).

The humerus bears numerous bite marks which lie on several points on both major faces of the bone (anterior and posterior). These are especially concentrated on the posterior face of the deltopectoral crest, and others are located on the proximal and distal ends of the bone (see Fig. 1). The hu-

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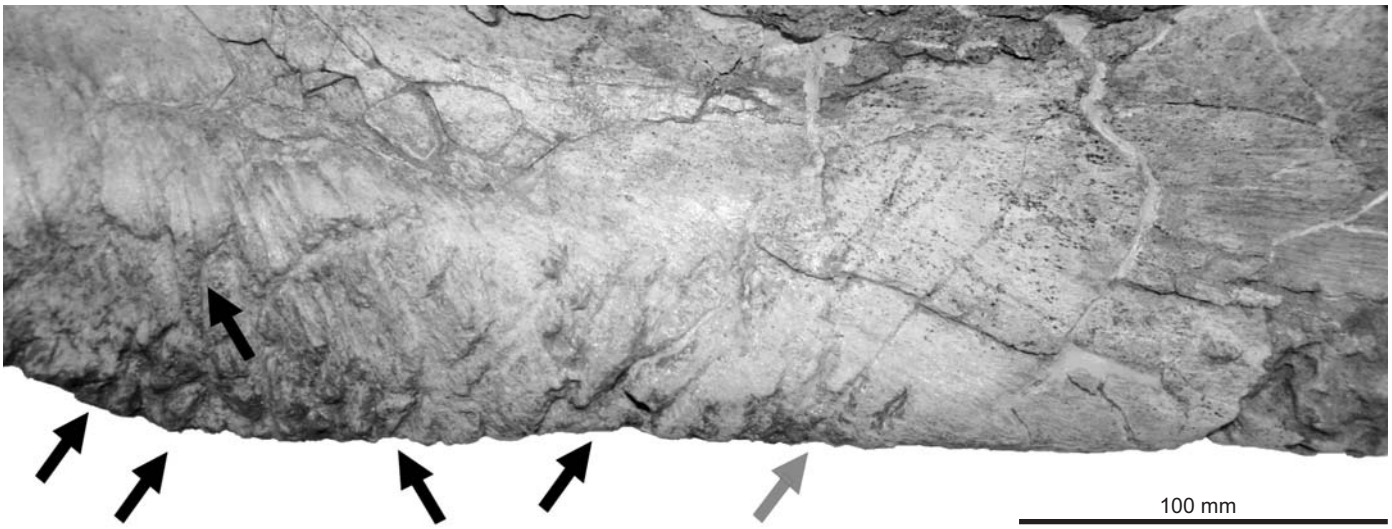


Fig. 2. Close up of the medial face of the deltopectoral crest of hardosaurid *Saurolophus* (MPC-D100/764) from the Maastrichtian Bugin Tsav locality in Mongolia. Black arrows indicate some of the drag marks left by the teeth of the theropod, with their orientation also indicated by the direction of the arrow. The grey arrow points to a bite and drag mark where a slight surface drag mark later goes deeper into the bone cortex close to the edge of the crest.

merus itself has suffered some minor surface damage from weathering, but none of this correlates in morphology with any bite marks or scrapes and is thus concluded to be the result of erosion and not a record of feeding. The surface of the bone is in good condition overall, making the marks clear and easy to identify. Bite marks take the form of three separate morphologies (though these are part of a greater continuum), and it is useful to provide rough working definitions of each as part of this description and for future work on bite marks. We are not aware of other formal classifications of bite-marks and thus this should serve as a useful model for future descriptions of other traces. These are based on the visible morphologies of the traces and the inferred behaviour of the animal during the biting that caused these marks.

Punctures.—These are simply deep bites that are sunk directly into the bone and penetrate the cortex of the bone (i.e., the bone was bitten and released, there was no, or only very limited, dragging or pulling by the jaws to create elongate traces). If these are of sufficient power and depth they may cause the bone to break off or fracture, causing additional damage. In some cases the punctures can strongly match the morphologies of the teeth making the marks, to the point where they can be identified as such. Puncture marks can be elongate in shape if they cut across the surface of a bone, but can still be typically distinguished from bite-and-drag marks.

Bite-and-drag.—Here the teeth are sunk into the surface of the bone and then pulled across it so that they leave scores in the bone. Again, if especially deep or repeated marks are made, the cortex may be pierced or fractured and separate, larger breaks may occur. These marks roughly correlate with the "puncture and pull" behaviour described by Erickson and Olson (1996).

Drag marks.—Here the teeth are placed only just on the surface and pulled such that only light marks are made that do not break through the cortex surface. This is obviously at the lower end of a continuum that can finish with very deep bite-and-drag marks, and in some cases individual traces can start as drag marks and then change into bite-and-drag marks as further power is applied, or vice versa as the power is released. However, the two are typically somewhat disjunct and distinguishable and thus these separate definitions are useful and practical. Drag marks and bite-and-drag marks are here collectively called "score marks".

The damage on the humerus can be broadly broken down according to the location on the bone, as damage is concentrated on the proximal and distal ends of the bone and the deltopectoral crest. The bite marks in each part are characteristic with a few deep punctures and grooves on the proximal and distal ends, and numerous scrape marks of both kinds on the deltopectoral crest. The humerus shows very extensive bite marks, representing numerous individual bite events on the bone. A minimum of fifteen can be identified, though the number is likely considerably higher. Marks can be made simultaneously from two or more teeth; thus, a scrape mark of four parallel grooves could represent only one mark or up to four separate ones.

Proximal end.—There are two large and deep bites restricted to the very proximal end of the humerus. One lies on the very start of the deltopectoral crest on the anterior face and consists of a pair of deep sub-parallel gouges that are probably puncture marks (18–35 mm long and 5 mm deep). The second consists of a pair of deeper holes (7 mm deep) across the anterolateral corner of the anterior end of the humerus. A possible third hole is present. Unlike almost all other bite marks on the bone, this feature lacks clear, clean edges implying parts of the bone cortex may have broken and flaked off as a result of the bite. It appears that the very edge of the bone was bitten hard and as a result the teeth largely penetrated the bone and gouged out these large marks. There

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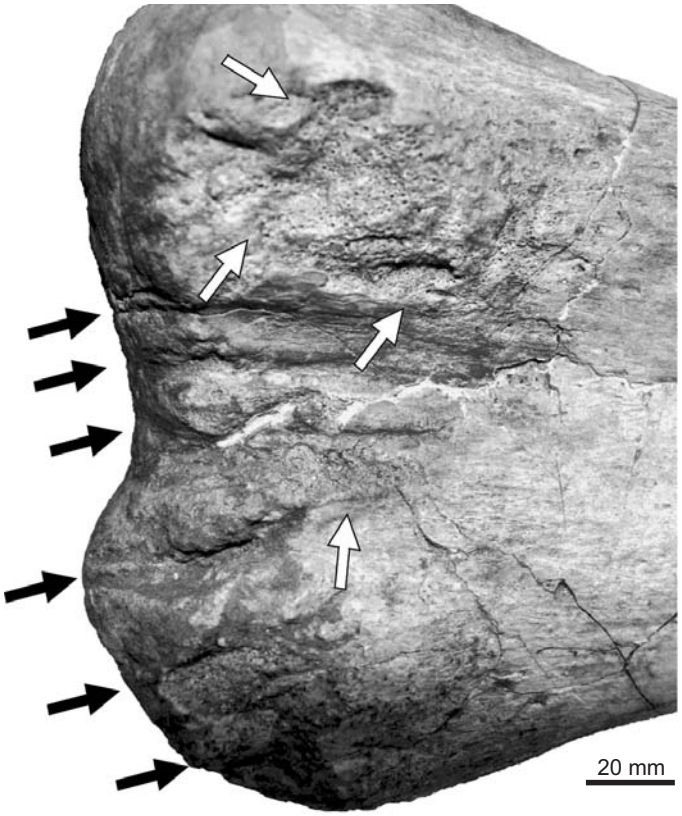


Fig. 3. Close-up of bite marks on the on distal end of left humerus of hadrosaurid *Saurolophus* (MPC-D100/764) from the Maastrichtian Bugin Tsav locality in Mongolia. Black arrows indicate deep scores that penetrate the cortex on the end of the bone. White arrows indicate deep puncture marks on the surface of the bone.

are correlating marks on the immediate reverse side of the crest coming across the edge of the bone towards the mark on the posteriorlateral face, which likely represents the teeth of the upper and lower jaws closing. The proximo-medial corner of the humerus is missing and there is also a relatively deep gouge in the centre of proximal end of the humerus, with a second shallower groove next to it on the anterior face, this damage may be feeding or from partial erosion.

Deltopectoral crest.—The deltopectoral crest shows extensive scrape marks of both the drag and bite-and-drag types (see Figs. 2, 3). The marks are concentrated on the distal part of the anterior face of the crest. On the posterior face there are at least three sets of scrapes visible—one pair of marks on the proximal half of the crest, and two sets on the posterior half (one of these consists of four individual grooves and the other of two or more). These latter sets cross each other at roughly right angles. In neither case are the marks especially close to the edge of the crest. None of these marks on the anterior face are especially deep or long (1–2 mm deep and up to 45 mm in length); they are considered to be drag marks. On the anterior face of the crest there are numerous score marks, both drag and bite-and-drag marks. All of these occur in the distal two thirds of the crest and terminate at the lateral edge of the crest. These bites represent at least six separate attempts by the predator to bite the bone, and possibly several more. They are oriented in two directions, again at approximately right angles to each other, with the bites overlapping each other. Many are relatively deep (5–9 mm in depth) and long (up to 70 mm long). They are especially concentrated in both number and density on the distal part of the crest, which has suffered extensive damage as a result.

Distal end.—The distal end of the humerus shows numerous deep bites that are a result of punctures that strip off parts of the cortex. These are considered very deep bite-and-drag marks (see Fig. 3) and are broadly similar to those seen at the proximal end. Several very large and deep scores lie on the anterior face of the humerus, both on the medial and lateral sides, and are up to 15 mm deep. On the lateral side, these marks extend onto the lateral face of the humerus, where more grooves are visible and parts of the cortex have been removed, presumably as a result of feeding. The traces continue as a series of deep (10 mm) bite-and-drag marks across the anterodistal corner and into the middle of the bone on the anterior face of the distal humerus. Additional cortex is missing on the anteromedial face of the distal end, probably through feeding as opposed to erosion (grooves are present despite the damage). These bites match those on the posterolateral corner and are interpreted as being produced by the two sets of teeth coming together during a strong bite.

Discussion

Taphonomy of the carcass.—The *Saurolophus* skeleton is largely complete and articulated with only some parts of the vertebral column and parts of the forelimbs missing, the hindlimbs are slightly displaced and the distal tail is folded over. The left humerus is located close to its natural anatomical position. The skeleton appears to have undergone very limited water transport and was buried quickly as the specimen is near complete, articulated and only the apparently exposed left humerus (see below) suffered any weathering and no bones suffered any apparent damage from tumbling or abrasion (Voorhies 1969).

A skeleton of *Tarbosaurus* (Theropoda: Tyrannosauridae) was also found in the same sandstone layer, close to the *Saurolophus* skeleton, during the same field season. The skeleton was also articulated but a number of elements were more widely dispersed and removed from their original position as compared with the *Saurolophus* skeleton. This suggests that the *Tarbosaurus* skeleton remained exposed much longer than the *Saurolophus* skeleton, although there are no apparent bite marks on the former to indicate scavenging.

The bite marks can be attributed to a scavenging event based on several lines of evidence. There is no evidence of large and obvious wounds which would indicate a predation event by a large bodied-carnivore. Nor would a large-bodied predator having an entire carcass to feed on have only left

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any traces on a single humerus. The pattern of carcass consumption by extant African carnivores (Blumenschine 1987) suggests that one would expect to see damage to the rear of the carcass first (the hindlimbs and chest cavity) before the less muscled forelimbs, but no such damage is apparent in the *Saurolophus* skeleton. This interpretation is complicated somewhat by the absence of other brachial elements (lower arm and manus bones plus the second humerus). It is likely that these were lost before the *Saurolophus* reached its final point, through violent transport as opposed to an alternative scavenging or predation event. Long arms bones are usually favourably recovered after transport (e.g., see Voorhies 1969) so this loss is odd, but far from impossible. The missing left brachial elements are not problematic, as they may have eroded subsequently (the humerus has suffered some damage) or been moved or destroyed by the scavenging animal but in neither case affect the interpretation of damage to the left humerus.

It would appear, therefore, that the *Saurolophus* died and suffered limited damage where it fell, or during water transport, and lost the right arm. Later it came to rest in a position on its right hand side and was buried leaving only the left arm free of the substrate. Only the left humerus has suffered any erosive damage unlike the rest of the skeleton which also free of bite marks, suggesting that it was buried and thus inaccessible to the scavenger of the event described here (or any others). The intact nature of the left humerus suggests that perhaps the similarly robust radius and ulna would not be destroyed during feeding though the bite marks at the ends of the bones suggests that the scavenger may have been attempting to remove them (but not necessarily consume them-see below) and this cannot be discounted.

Identity of the bite maker.—The bite marks on the *Saurolophus* humerus can be referred to the derived tyrannosaurid *Tarbosaurus* for a number of reasons. First, the shape, pattern and depth of the puncture feeding traces on the humerus closely match those of *Tyrannosaurus* (see below for details), recovered as the sister taxon to *Tarbosaurus* in many phylogenetic analyses (Holtz 2004; Sereno and Brusatte 2009), implying that they were made by a large tyrannosaurid. The structure of the tooth marks, which preserve only rare serrations, is also similar to that of described tyrannosaurid marks (Erickson and Olson 1996) and the spacing between the marks of individual teeth (>1 cm for some) for single bite marks imply that a large predator was involved. Further evidence for a large predator includes the large size and deep depth of the bite marks. Another tyrannosaurid, *Alioramus*, is also known from the Nemegt Formation, but it lacks the adaptations for powerful biting that are present in *Tarbosaurus* and was a generally smaller animal (see Brusatte et al. 2009) and thus is an unlikely candidate for the trace maker here. Additionally, both teeth and skeletal material of *Tarbosaurus* have been found at the same locality and horizon as the *Saurolophus* skeleton, and thus this carnivore was certainly present in the area. (It is unlikely that this specific associated animal was the scavenger in question as it is rather more disarticulated than the *Saurolophus*, implying a different taphonomic history). At the absolute minimum we can confidently say that a large predator, most likely *Tarbosaurus*, fed at least once on the hadrosaurid *Saurolophus*. However, the nature of the material is such that we can infer several other details of behaviour.

Comparison to other tyrannosaurid bite traces.—The overall nature of the bite marks is comparable to those feeding traces described for *Tyrannosaurus*, but different in detail. The best and most detailed example of *Tyrannosaurus* bite marks comes from the *Triceratops* pelvis described by Erickson and Olson (1996), which shows numerous deep bite marks and punctures but only a few limited scrape marks (though these are commonly seen in other theropod feeding traces; e.g., Jacobsen 1998; Chure et al. 2000). This is remarkably similar to another specimen where a large tyrannosaurid had also fed on a large ceratopsid pelvis leaving puncture, but few scrape marks (Fowler and Sullivan 2006). Although there are some deep penetration marks seen on the *Sauropolophus* (of similar depth to those noted by Erickson and Olson 1996), the dominant traces are clearly scrape marks, and especially shallow drag marks, while scrape marks were absent on the *Triceratops* specimen. In the case of the *Tyrannosaurus–Triceratops* association, there were large and deep bite and drag traces and punctures, but on the humerus the bite and drag marks are fewer and far shallower (only 1–2 mm, as compared to over 11 mm). This may reflect a difference in feeding style between the two taxa, different feeding forces, or more likely may simply represent different circumstances surrounding the two feeding events (i.e., different bones, with differing shapes and muscles masses, accessible in different ways).

Although Erickson and Olson (1996) did not specify whether they considered the *Triceratops* pelvis bite marks to reflect a predatory or scavenging event, the latter would seem more likely given that it appears to represent a very late-stage carcass consumption. This is also the case with the Fowler and Sullivan (2006) specimen where they inferred scavenging. In both cases, a single, large, complex and robust element (a neoceratopsian pelvis) was present and was attacked with numerous large penetrating bites. Again, comparisons with patterns of carcass consumption in extant carnivores would suggest that a pelvis-sacral complex would not be the first choice for consumption, and despite the abilities of tyrannosaurids to attack and consume bone (e.g., see Hone and Rauhut 2010 for a review of this topic) one would not expect a feeding tyrannosaurid to commit such efforts to this part of the body with repeated deep-bone bites if large blocks of muscles were available. Thus both the part of the carcass being attacked and the manner of that attack would favour late stage carcass consumption, which would imply scavenging. The isolated nature of the ceratopsian pelves (no other associated bones were identified) suggest that this interpretation is correct.

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However, evidence for scavenging of the *Saurolophus* carcass is more definitive that either of these examples. In contrast to the pelves examples, the carcass is comparatively well-preserved and articulated, with the only visible damage from feeding sustained to the left humerus. This implies the absence of any additional significant feeding or scavenging before the event documented here. More muscle was present elsewhere on the hadrosaurian body than on the forelimbs, implying that little more than the arm was exposed for the tarbosaur to feed upon. However, the feeding behaviour in each instance is difficult to compare, as the generally simplified morphology of the humerus would have been more amenable to scrape feeding to remove flesh than that of a ceratopsian pelvis-sacral complex, perhaps explaining the dominance of scrape marks on the *Saurolophus*. Clearly, both feeding types (punctures and scrapes) fall within the envelope of behaviours for large tyrannosaurids, though others may also have been employed in different situations.

Inferred behaviour of the bite maker.—The details of the bite marks and their pattern provide information on the feeding method employed by the scavenger. Although some deeper punctures on the humerus can be aligned on the anterior and posterior surfaces, suggesting that these were made by the use of the upper and lowed jaws together during biting, the scrape marks on the main faces of the bone cannot. Since the scrape marks left on the anterior and posterior surfaces of the deltopectoral crest are not sub-parallel to each other, they cannot have been made by the action of the upper and lower jaws in unison. Moreover the great discrepancy in the number and depth of the scrapes on the two faces suggest that these were produced separately through the action of one set of teeth alone.

We conclude that these were made by the teeth of the upper and not lower jaws because of the way the traces are packed so closely together on the *Saurolophus* specimen. This correlates well with the dental morphology in derived tyrannosaurids (and indeed theropods in general)—the teeth of the premaxillary dental arcade are less widely spaced (e.g., see Brochu 2003) in a way that the teeth on the dentaries, where they meet, are not (DWEH personal observation). The inferred large body size of the carnivore (as seen by the power required for the puncture marks) rules out these are being, say, dentary teeth from a smaller animal. The scrape marks are also typically in sets of two to four marks which again likely represent the tyrannosaurine premaxillary arcade. It would also be easier for the animal to simply place its top jaw on a bone and draw the teeth across it to remove flesh than to try and do so with the lower jaw. The scrape marks were probably not made by the lateral teeth of the maxilla or dentary being applied to the humerus and then pulled laterally, as in this case the marks would be more widely spaced, the marks would likely be less clearly defined (the lateral teeth are more blunt), the marks would be more numerous and spread over a larger area, and the actual process of applying the teeth and forces in this way would likely be far harder for the animal to achieve.

We therefore conclude that the majority of these scrape traces were made using the upper jaws alone to produce these marks, and that strong bites using the upper and lower jaws in concert were not performed here on the flat surface of the bone. Given that the marks occur on both sides of the humerus and were presumably done in both cases by the upper jaws alone, then the humerus was perhaps freed from the carcass before, or more likely during, feeding to provide this access to both sides. However, as the humerus was found in a position, with respect to the rest of the skeleton, close to the natural articulation point, is it questionable as to whether or not the humerus was separated from the carcass by the scavenging *Tarbosaurus*.

The bites on the humerus are concentrated in several areas and the traces vary according to their location, which implies a deliberate and varying feeding strategy on behalf of the theropod. There are deep bites around the proximal and distal end of the humerus, as well as much deeper bite-and-drag marks. This was likely an attempt to remove the cartilage cap which surrounds the ends of long bones in large, heavy animals and/or to separate the individual bones at the joints. This again suggests this was a scavenging event, as surely other, more meat-rich parts of the skeleton would have been preferable targets for feeding. In contrast, the brachial muscles would have been attached to the deltopectoral crest of the humerus and this would be an obvious target for scrape feeding to remove the muscle tissue that was available for consumption.

It is notable that the deepest punctures and bites on the humerus are in excess of 12 mm in depth, which, had they occurred on the deltopectoral crest, would probably have been sufficient to crack or break off at least part of the crest (it is between 18 and 30 mm in thickness). The animal could therefore have probably removed the deltopectoral crest in whole or in part through simply biting it off of the humerus and consuming it. Tyrannosaurids have been known to consume large amounts of bone (with considerable oral processing sometimes taking place; Chin et al. 1998), though not necessarily large single pieces of bone, so here this appears to be an active choice to continue with scrape feeding as opposed to biting through the crest as a whole (or even attempting to do so) when it was capable. The presence of the scrape marks on both sides of the deltopectoral crest suggest that the humerus was free of the carcass or that at some point during feeding it was turned over so that the anterior face was accessible. If the bone was free, it moved little since it was found close to the point of natural articulation on the skeleton.

The humerus may have remained articulated with the carcass (or perhaps only loosely attached through a few remaining tendons, etc.) despite the efforts of the scavenger to free the bone entirely. The idea that the deep bites on the proximal and distal ends were intended to separate the joints is consistent with the available evidence. If the ani-

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mal were able to separate the joints this would facilitate feeding by allowing oral processing of individual bones or whole sections of limbs (e.g., the lower arm as a unit). This would also facilitate scrape feeding on multiple surfaces and also allow the scavenger to remove cartilage bone caps for consumption.

The deep bites on the proximal and distal ends are here inferred to have been performed by the anterolateral or anterior teeth. Simple lever mechanics would suggest that a more powerful bite can be delivered by teeth at the rear of the jaw those at the front, (although bone-breaking bites can still be produced by the anterior teeth of tyrannosaurines; see Carpenter 2000). However, it would be difficult for a tarbosaur to maneuver its jaws around the joint at either the shoulder joint or the elbow joint, to bite at the joint with the posterior teeth in the jaw. Simply using the premaxillary teeth or anterolateral teeth in conjunction with the mandible would be easier. Although both the left scapula and radius/ulna are missing, it seems improbable that multiple bites could have been inflicted by the posterolateral teeth without leaving other puncture marks on the humerus, and none are visible.

The pattern of bites seen here suggests that at least some theropods were probably skilled at removing muscle and other tissues from carcasses, and that the idea of them as crude butchers biting through and consuming large portions of the prey is incorrect (e.g., Paul 1989: 32). It is doubtless that some theropods occasionally inflicted severe damage to bones during feeding (as with the *Triceratops* pelvis), but this appear to be a matter of choice and not a result of a lack of ability. Although even large bones could be cracked and broken and consumed when desired, this was not necessarily a fundamental part of tyrannosaurid feeding.

Conclusions

Overall, this new trace fossil provides much new information about tyrannosaurid feeding behaviour. There has been much debate as to whether tyrannosaurids were scavengers or predators (e.g., see Holtz 2008 for a review), and although nearly all extant predators combine varying levels of scavenging with predation, this single event can be marked down confidently as a tyrannosaurid scavenging from a hadrosaurid carcass. The pattern and distribution of the feeding traces on the bone in question can be used to infer feeding patterns and extends our knowledge of tyrannosaurid behaviour. Clearly on at least some occasions, feeding was highly selective and directed at the prey item in a deliberate manner. The variation between feeding on the distal ends of the humerus and the deltopectoral crest demonstrate a variation in technique, probably due to the different types of soft tissues to be extracted and the shape of the part of the bone being fed upon.

The traces also suggest the dominance of scrape feeding, performed by the premaxillary dental arcade, for extracting muscles tissues and that the lower jaw was largely unused for this technique. This represents active selection of the feeding method employed by the carnivore, something not previously recorded or determinable in theropod feeding traces. Finally, we provide further evidence of tyrannosaurids feeding upon (though not necessarily predating) adult hadrosaurids.

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