Difficulties in assigning trace makers from theropodan bite marks: an example from a young diplodocoid sauropod

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Bite marks on the bones of dinosaurs are relatively rare for non-tyrannosaur dominated faunas, and few have been described in detail. Here we describe a femur of a young diplodocoid sauropod in the Carnegie Quarry (Late Jurassic Morrison Formation) at Dinosaur National Monument that shows extensive bite marks to the proximal part of the bone. This is the only record of bite marks from this extensive quarry of over 1500 vertebrate elements, making this a most unusual find. Identification of the trace maker is difficult as multiple large theropods are known from the quarry. Furthermore, we show that subtle different actions of feeding can potentially result in very different spacing of bite marks making matches to tooth patterns in the jaws of potential bite makers very uncertain. Although identification is uncertain, the trace maker is clearly not a tyrannosaurid but the selective scrape feeding pattern seen here is similar to the of tyrannosaurid theropods. This technique may be more widely distributed among large carnivorous theropods than previously realised.

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1 Introduction

Identifying interactions between long extinct non-avian dinosaur (hereafter simply ‘dinosaurs’) species is a key part of reconstructing trophic levels and foodwebs, and of the possible structure and function of ancient ecosystems. In addition, this may also help improve our understanding of the behavior of these animals. However, this is naturally a difficult prospect – direct evidence is typically limited to bite marks (Hunt et al. 1994), stomach contents (e.g. Charig & Milner 1997) and coprolites (Chin 1997) - though other sources are occasionally available (e.g. DePalma et al. 2013) and it is often difficult or even impossible to identify even one, let alone both, of the species involved. All of these sources within the dinosaurian fossil record are rare and although bite marks are by far the most common of these (e.g. see Jacobsen 1998), it can be difficult to correctly identify the trace maker when multiple possible candidates are known.
Identification of bites can be best attributed when shed or embedded teeth are found in association with bite marks (e.g. Currie & Jacobsen 1995; Hone et al. 2010; Xing et al. 2012). However, the size and shape of the marks may be indicative in some circumstances such as in the case of *Tyrannosaurus* (Erickson & Olson; 1996) where it is the outstanding large carnivore in its environment. Tyrannosaurids produce a disproportionate number of bite marks on bone compared to other theropods (Fiorillo 1991; Jacobsen 1998) and represent most of the few theropod bite marks that have been described in detail. Therefore, new evidence of bite marks from non-tyrannosaurid dominated faunas are potentially important in assessing the behavior and ecology of dinosaurs in ecosystems.

In marked contrast, bites from non-tyrannosaur dominated faunas are rare (Hone & Rauhut 2010). Despite the large numbers of specimens from other formations, such traces remain rare but also little studied. Even in the well-known Morrison beds, only a limited set of works have looked at bites in detail (e.g. see Matthew 1908, Hunt et al. 1994; Carpenter 2000; Carpenter et al. 2005; Chure et al., 2000) making any new find important for understanding non-tyrannosaurian theropods.

Here we describe the bite marks from a large and indeterminate theropod on the femur of a juvenile diplodocoid sauropod in the Carnegie Quarry of the Morrison Formation (Figure 1). The bites are unusual as this is the only one identified with theropod bite marks from over 1500 vertebrate elements in the quarry. The nature of the taphonomy of the preserved femur is unusual but there is some evidence of the selective feeding strategies also seen in tyrannosaurs. We note that assigning a likely
candidate of the tracemaker is especially difficult here. There are numerous large theropods present in the Carnegie Quarry with likely similar feeding apparatus, and we show that the size and spacing of bite marks may be difficult to align with premaxillary arcades.

1.2 The Morrison Formation

The sediments of the Late Jurassic Morrison Formation are distributed over $1 \times 10^6$ km$^2$ across nine states in the Western US (Dodson et al. 1980). This formation represents a mosaic of fluvial, lacustrine (including large hypersaline lakes), and floodplain environments whose pattern of distribution shifted geographically during the nearly 7 million years of Morrison deposition. Isotopic dating of $^{40}$Ar/$^{39}$Ar from near the base and high in (although not at the top of) the Morrison yields dates of 156.84±0.59 and 150.00±0.52 Ma respectively (Kowallis et al. 1998, as recalibrated by Trujillo & Kowallis 2015). These dates correspond to a Kimmeridgian through mid-Tithonian age (Ogg & Hinnov 2012).

The Morrison is world renowned for its exceptional paleontological richness of fossil vertebrates, especially that of dinosaurs (Turner & Peterson 1999; Chure et al. 1998, 2006). As a result, it has long attracted the attention of earth scientists and paleontologists going back into the mid-19th century. The formation has been critical both to our understanding of dinosaur morphology and diversity as well as insight into Mesozoic terrestrial ecosystems (Ostrom & McIntosh 1966; Foster 2003; Turner & Peterson 2004). There are numerous large, dinosaur dominated, bones beds that have
yielded many tens of thousands of dinosaur fossils, ranging from isolated bones to spectacularly complete skeletons with skulls. Of these bones beds, the Carnegie Quarry is unique and a first among equals because of it being the specific resource for the creation of a national park and its in-situ fossil display.

1.3 Locality Information

The Carnegie Quarry (CQ, Dinosaur National Monument, Utah, U.S.A.), in Dinosaur National Monument, is located approximately 11 km north of Jensen, UT (Figure 2). In the area of the CQ the Morrison is 204 m thick and quarry is 167 m above the base of the formation (Bilbey et al. 1974). It is situated in the Brushy Basin Member, the uppermost member of the Morrison in this area. Although the quarry has been extensively excavated and much of the sandstone layer has been completely removed, a significant part of the quarry sandstone, with in-situ exposed bones, is enclosed within the Quarry Exhibit Hall. DINO 5119 (Dinosaur National Monument, Jensen, Utah, U.S.A.) is in the extreme SE corner of the exposed bone bed, about 5 m west of the east foundation wall and 1.5 m above ground level. This area contains one of the densest accumulations of bone in the present day CQ.

1.4 The Carnegie Quarry at Dinosaur National Monument

The Carnegie Quarry is situated in the Brushy Basin Member of the Late Jurassic Morrison Formation in NE Utah, USA (Turner & Peterson 1999). Discovered in 1909 by Earl Douglass of the Carnegie Museum, it is one of the major dinosaur quarries in
the Morrison (McIntosh 1977; Dodson et al. 1980; McGinnis 1982) and was the specific site for which Dinosaur National Monument was created in 1915 (Presidential Proclamation 1313). Although extensive excavations took place between 1909 and 1924, the quarry today preserves some 1500 vertebrate bones, exposed in-situ, in a 60° dipping sandstone bed within the Quarry Exhibit Hall (McIntosh 1977). The CQ is unusual in its tripartite nature, having had many years of excavation and removal of vast numbers of fossil bones, a very large part of the bone bed with fossils exposed in-situ and enclosed within a building (Quarry Exhibit Hall), and a very large part (to the east of that building) exposed on the surface with no overburden and subjected to little fossil excavation. These three different datasets of the same bone bed offer many research opportunities.

The most recent study on CQ deposition identifies several episodes of rapid deposition in a braided river system reminiscent of the Platte River in NE., USA (Carpenter 2013). The quarry fauna and flora is composed of ten genera of dinosaurs, one genus each of goniopholid crocodylian and sphenodontian, two genera of chelonians, as well as abundant unionoid clams and unidentifiable carbonized plant remains. Although biased in favor of large specimens, it has yielded significant juvenile dinosaur material, only some of which have been described (Gilmore 1925a, b; Galton 1982; Whitlock et al. 2010; Melstrom et al. 2016).

Recent recalibration of a previously published 40Ar/39Ar isotopic date yields a value of 150.91 Ma) for a volcanic ash immediately below the quarry sandstone (Kowallis et al. 1998; Trujillo & Kowallis 2015). Balikova (2014) reports a
magnetostratigraphic age of Late Tithonian for the quarry sandstone corresponding to the marine sequence magnetic anomaly subchron CM22n.3n (148.72-148.79 Ma).

2. Description

The bite marks are located on the lateral side of the anterior face of a right femur of a small sauropod specimen (cataloged as DINO 5119 – Figure 3). Although occurring in a part of the quarry with many bones, it is not overlapped by any. As a result, DINO 5119 has been completely exposed in anterior view and its full outline is visible. The element is generally well preserved and in good condition, though, as with many other bones in the quarry, some of the cortex is damaged and missing from the bone, including the anterior face of the medial condyle and the anteriomedial part of the femoral head. There is also a repaired crack across the proximal part of the shaft, but with no bone loss. The femur is 583 mm long, and 81 mm wide at the narrowest point of the shaft. The proximal width is 166 mm and the width of the distal end is 183 mm.

Approximately 1 m from DINO 5119 there is a left femur of a similarly sized sauropod (DINO 5088), which almost certainly belongs to the same individual as 5119 based on their proximity and general similarity of size and form, but this cannot be absolutely determined.

The identity of DINO 5119 is difficult to ascertain, though it is likely a diplodocoid. The femur is considerably smaller than that of any adult sauropod identified in the Morrison suggesting it belongs to a young animal. A nearly complete
and articulated *Camarasaurus* skeleton from the CQ (CM 11338, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.) is only about one-quarter adult size, and its femoral lengths (550 mm right, 530 mm left) are only slightly less than that of 5119 (Gilmore 1925a). This strongly implies that DINO 5119 is immature (though see Wedel & Taylor 2013 and Hone *et al.* 2016 on the difficulties of identifying the ontogenetic status of sauropods). Dwarf sauropod taxa (less than 5 ton adult body weight) are very rare and associated with island habitats (Sander *et al.* 2006) and not the center of a continent-sized landmass.

The diplodocoids are the most common sauropods in the in the CQ, *Apatosaurus louisae, Barosaurus lentus,* and *Diplodocus longus* (Holland 1924; Gilmore 1932, 1936; McIntosh 2005) but the high diversity of the sauropods known from the Morrison Formation (Farlow *et al.* 2010) means that other credible candidates are also possible, if less likely. Two features distinguish the femur of Morrison diplodocoids from that of the macronarian *Camarasaurus,* the only other CQ sauropod. In diplodocoids the tibial condyle is elongated (Foster, in Wilhite 2005) and the fourth trochanter in diplodocoids is more proximally placed than in *Camarasaurus.* Unfortunately, these features are clearly seen only in posterior aspect, an inaccessible view for the in-situ DINO 5119 and its likely pair 5088. However, close inspection of the exposed medial edge of the femur in 5119 indicates that the fourth trochanter is on the proximal one third of the femur, indicating diplodocoid affinities.

The femur of an adult *Apatosaurus* is more robust than in adults of *Diplodocus* and *Barosaurus* (Wilhite 2005). Ontogenetic growth of limb elements in sauropods is
isometric so this difference holds for juveniles as well (Tidwell & Wilhite 2005).

DINO 5119 is gracile as in Diplodocus and Barosaurus. However, the limbs of Diplodocus and Barosaurus are difficult to differentiate without associated forelimb and hindlimb ratios (McIntosh 2005; Wilhite 2005), so given the isolated occurrence of 5119 we cannot further refine its affinities.

2.1 Bite marks

Multiple marks are present across DINO 5119 (see Fig 3). Most consist of a series of short traces (under 50 mm in length) that are subparallel to one another. Following Hone and Watabe (2010) these traces are all considered to be ‘drag marks’ as they do not puncture through the cortex. There is some fragmentation of cortex at the dorsal edge of the bone which gives the appearance of very deep bites, but this may be a result of erosion at the point of the bites leading to fragmentation of the bone in this area. There are no obvious punctures on the bone (sensu Erickson & Olson 1996; Hone & Watabe 2010) although there are three subcircular indentations in the bone on the midshaft of the bone these do not match known theropod bite marks and their origins are unclear.

Alternative origins for the marks beyond bites can be ruled out. DINO 5119 was exposed in-situ in 1984. Preparation was done with airscribes and hand tools by experienced preparators. Of the 1500 bones exposed in-situ in the quarry sandstone none show gouging preparation tool marks, and even features such as delicate traces of osteophagus insects have been exposed without damage (Hasiotis et al. 1999; Oser &
Chure 2016). Hardness of the sandstone varies both across the quarry sandstone and stratigraphically within it, but separation from the bone is generally good. The sandstone in the area of DINO 5119 and 5088 is among the most friable in the quarry, to the extent that it sometimes presents problems of stability that threaten bones with falling out of the rock. Thus the preparation of DINO 5119 would be easier than in most other areas of the quarry sandstone. All these facts support our interpretation that the marks seen on DINO 5119 are tooth traces and not preparation artifacts.

A number of different orientations of marks are present indicating that there were multiple bites on the bone, but the exact number is hard to determine. There are at least two different sets of marks (A-G and H, I, K, M-O) and each trace has been given an identifying letter (see Figures 3 and 4) for clarity. Measurements of each mark are presented in Table 1.

The traces designated A-G are all subparallel to one another and run diagonally from the dorsal lateral corner of the medial face of the bone. Marks A and B go deep into the cortex and are part of a rough area of damage to the cortex. This damage may be a result of these bites (see below). Of the two, trace A in particular is poorly delimited and it is not clear if this is a deep bite or one that has been exaggerated by further erosion or breakage. Mark B is more clearly defined deep groove, but also shows much breakage of the bone around it. As with trace A, trace B is far wider and with indistinct margins compared to most described theropod bites.

Marks C and D also show fragmentation of the bone towards the dorso-lateral margin of the bone both more medially show clear drag marks across the surface of
the bone. The origins of marks (based on the tapering of the marks away from these points) for E, F and G lie more medially on the bone than A-D but are mostly shorter and all are clearly defined.

A second group of marks lie almost parallel to the long axis of the femur (H, I, K, M-O). These are much less deep than those of A-G and are mostly short, although mark H is long and crosses a number of other bites. The marks M, N and O are close together and subparallel to one another, although N is rather longer than M and O as it continues below the break in the bone. It is also possible that N is continuous with H (see Figure 3) given its position and orientation.

Some other short and shallow marks (designated J, L, P, and Q) are present that may potentially align with either of the above sets, or be independent of them. Mark J may be an extension of F though it is parallel to F and thus may be a mark from a different bite. Q lies to the side of the set M-O and is also at a different angle suggesting it is a separate trace. Three small grooves (collectively designated R) lie at the midpoint of the shaft though still on the anterior face of the femur.

3. Discussion

3.1 Trace maker identity

Although theropods make up a small percentage of the CQ dinosaur fauna, there are multiple candidates for the bite-maker that known from the quarry. *Allosaurus* is the most commonly preserved taxon, but *Ceratosaurus* and *Torvosaurus* are also
known from limited, but diagnostic, material (Madsen & Welles 2000). Other
theropods from elsewhere in the Morrison Formation (e.g. Marshosaurus,
Ornitholestes, Saurophaganax, Stokesosaurus see Weishampel et al. 2004) are
currently unknown from the CQ and while they cannot be easily ruled out, are not
considered further here. A crocodyliform – Goniopholis – is also known from the
quarry but its relatively low maximum size (jaws typically less than 500 mm in length
– Foster 2006) and the lack of subcircular punctures or splintered surfaces associated
with scores on the bone as seen with modern crocodilian feeding traces (Naju &
Blumenschine 2006; Boyd et al. 2013) suggest it is not a credible candidate as the
trace maker and so is not considered further here.

In the absence of shed teeth, the main features available for identification are the
depth, width and spacing of the marks. Each of these has potential issues when trying
to match them to candidate trace makers in addition to the obvious issue of
intraspecific variation of each taxon, and especially of size through ontogeny. Bite
marks that represent feeding traces by theropods can usually be assigned to
premaxillary teeth where there might be maximum control for the animal using teeth
at the front of the jaw, and thus this series are the most important to consider, although
maxillary teeth may potentially be involved in some bites.

The premaxillary tooth counts for taxa known in quarry are five per side in
Allosaurus (Madsen 1976), and three for Ceratosaurus (Madsen & Wells 2000). Britt
(1991) lists the premaxillary tooth count in Torvosaurus as “3 (possibly 4)” in the
diagnosis (1991, their page 10). However, in the description Britt gives it as three
(1991, their page 13) and his fig. 3E (1991) shows only three. Although only three alveoli are present, he suggests that a slight depression behind the last alveous could be an additional alveolus lost during ontogeny.

The maxillary teeth of *Allosaurus* and *Ceratosaurus*, although diagnostic, are similar for a number of metrics compared to the known variation of theropod teeth (e.g. see Smith et al. 2005) and there are also some similarities in the proportional size and arrangement of teeth in the skull (Henderson 2000). However, premaxillary teeth in *Allosaurus* and *Ceratosaurus* differ not only in number but in morphology (Madsen 1976; Madsen & Welles 2000; Britt 1991). Premaxillary tooth crowns in *Allosaurus* are somewhat D-shaped in cross-section (although the lingual face is slightly convex) and the crowns are straight. Premaxillary teeth in *Ceratosaurus* are more circular in cross-section and recurved lingually. The outline of the premaxillary alveoli in *Torvosaurus* incates the teeth were more oval in cross section. *Ceratosaurus* differs from *Allosaurus* and *Torvosaurus* in having several well developed apicobasally oriented ridges on the lingual face.

Premaxillary teeth in these taxa are also different in their orientation in their respective premaxillae (Britt 1991). In *Ceratosaurus* and *Torvosaurus* the labial side of each alveolus is overlapped by the alveolus posterior to it, although to a much greater extent in *Torvosaurus*. *Allosaurus* usually lacks overlap of alveoli but when it is present it is small the alveolus overlaps the lingual side of the next posterior alveolus. These differences may well reflect different feeding strategies and might, in the future, prove useful or even diagnostic for identifying the tooth trace makers.
However, that will require more detailed formal descriptions and comparisons first. There are several known deep bites into or through bones (Hunt *et al.* 1994;, Chure *et al.* 2000; Carpenter 2005) preserved in the Morrison Formation that can be attributed to large-bodied theropods. These include bites in excess of 5 mm in depth (Chure *et al.* 2000), and although the exact size and identity of the animals that inflicted these marks is unknown, it is clear that at least some locally present theropods could produce bites deeper than those seen here on DINO 5119. Rayfield (2005) examined the possible mechanics of biting in *Allosaurus* and showed that it was less well suited to leaving bites than large tyrannosaurines. However, this does not rule out biting through bones, and in the absence of comparative studies of other Morrison theropods this is sadly uninformative as to the possible identity or otherwise of the trace maker. Similarly, Snively *et al.* (2013) suggested *Allosaurus* was well adapted to produce a bird-like ‘posterior pull’ feeding style which may fit with the long scrape marks here but does not necessarily rule out other candidates. Collectively therefore, bite depth and shape provides no definitive information to assist in identifying a possible trace maker.

The relative width of individual marks that should reflect the width of a single tooth that produced them, is also of limited value. Although *Allosaurus*, *Torvosaurus* and *Ceratosaurus* are homodont (at least compared to derived tyrannosaurs e.g. see Smith *et al.* 2005), they would have had different sized teeth in the jaws of individuals, and animals of different sizes would have different sized teeth relative to other conspecifics. The width of a single trace could potentially be used to determine the
size of the tooth that made the mark, but overlapping sizes and issues such of degrees
of wear on the tooth crown could also affect the size of a given tooth (the angle of use
could be a still greater issue, see below). In any case, although the teeth of these three
theropods do differ in terms of details such as degree of curvature and denticle counts,
there is currently no known relationship of this to trace shapes. The gross morphology
of the teeth (laterally compressed and recurved) is similar in all three taxa.

Finally, the spacing between individual tooth marks and their apparent size in
combination may give an indication at least of the size of an individual trace marker.
However, again there are potential complications here. Although some putative
theropod bite marks show the teeth moved in arcs across the face of a bitten bone (e.g.
Hone *et al.* 2010 c.f. feeding traces of some extant reptiles – D’Amore &
Blumenschine 2009, 2012) the vast majority seem to be simple straight ‘pulls’. These
actions leave straight lines, or sets of sub-parallel lines (e.g. Hunt *et al.* 1994; Currie
& Jacobsen 1995; Jacobsen 1998; Rogers *et al.* 2003; Hone & Watabe 2010) as traces,
such as seen here. This latter biting style should place the minimum amount of stress
on typical theropod teeth (at least the maxillary and dentary teeth) as it would align
the stress with the long axis of the cross-section of the tooth. However, even
thin-toothed reptiles apparently use the ‘medial-caudal arc’ feeding strategy when
teeth are contacting bone, (D’Amore & Blumenschine 2009) suggesting that this was
not necessarily a limitation of theropod feeding with tooth-bone contact. Even so, the
rarity of bites from non-tyrannosaurian theropods suggests that these animals often
avoided tooth-bone contact (Hone & Rauhut 2010).
Even if the jaws were moving such that the stress was delivered close to parallel to this axis of the tooth, small changes in the angle at which this is delivered could change the spacing between individual marks (Figure 5), and more dramatic changes in angle could leave very closely spaced marks for even widely spaced teeth. The spaces between individual scrapes might therefore be considered a useful minimum for tooth spacing, but multiple overlapping bites by one animal may occur (e.g. Hone & Watabe 2010) and it is likely difficult or impossible to tell one bite from multiple bites when only a small number of traces are seen as with DINO 5119. The three subparallel scrapes could represent one bite of three teeth, one of two teeth and one bite of one tooth, or one tooth applied three separate times.

Furthermore, these issues would be compounded by the absence of any teeth in the tooth row. Loss from feeding or simple replacement or other factors such as injury could lead to large gaps between teeth and thus artificially inflate the observed gaps between individual scrapes. Similarly, if a given tooth is at an odd angle in the mouth (and this does happen in some theropods as show by ablation and tooth-on-tooth wear on the lateral (ligual or labial) side of teeth e.g. see Schubert & Ungar 2005) may mean that the apices of two teeth are much closer together or further apart than would be expected normally and add further variations in the spacing of bite marks.

Similarly, bites delivered at an angle (e.g. Figure 5A vs 5C) could affect the width of individual traces. Even at the tip, the teeth of large Jurassic theropods are broader on their lateral than posterior faces. Thus a drag mark produced by the same tooth drawn at an angle would produce a wider trace than one drawn directly backwards.
Therefore, the breadth of a drag mark may not be a good indicator of tooth size, and fracturing of the cortex or erosion may further change the shape.

In short, it is not possible to make a confident attribution to one of the candidate theropod genera here. There are multiple possible trace makers, each of which is similar to the others in overall size and gross dentition and with no obvious differences in known in bite power. The width and depth of the traces here do at least suggest a large bodied theropod (they are considerably larger than are known from small bodied animals, e.g. Currie & Jacobsen 1995) which rules out smaller Morrison taxa, or juveniles of larger ones. *Allosaurus* is the most common theropod in the CQ and is also by the far most common theropod in the Morrison, with number of individuals swamping those of other theropods in term on occurrences in quarries or geographic and stratigraphic distribution (Foster & Chure 1998; Foster 2007). Based simply on the considerably greater prevalence of material, *Allosaurus* is the best candidate, but this is an extremely tentative assignment.

It is beyond the scope of this paper to assess individual patterns of marks left by different arrangements of teeth or different patterns of marks left by drags in different directions, but this is likely to be a promising area of investigation for future identifications of trace makers. Similarly, the widths of individual drag marks and their relationships to given teeth may show some currently unappreciated pattern.

### 3.2 Behaviour

Determining the difference between scavenging and a predatory event is difficult
for Mesozoic specimens, even when the taphonomic history is well understood and the marks are clear. In this case, the signals are mixed and somewhat confused. The exact taphonomic history of DINO 5119 is not known, but the general evidence of rapid deposition in a river system, coupled with the disarticulated nature of many specimens (including this one) does suggest at least some transport. The lack of other elements (DINO 5088 aside) and disarticulation of the femora do also suggest that the elements of the carcass are no longer in their original positions. Breaks in the bone and damage to the carcass may also be linked to transport.

The bites are primarily localised on areas of the femur where major muscle groups attach – the *M. iliotrochantericus caudalis* on the dorsolateral corner of the proximal femur, and the *M. femorotibialis lateralis* along the anterior face. This implies some level of selective feeding as seen in tyrannosaurs (see also Hone & Watabe 2010). The limbs are areas where carnivores are likely to feed first on a fresh carcass (Blumenschine 1987) as there is extensive muscle mass present perhaps suggesting an early stage of carcass consumption either from a kill by a predator, or scavenging of a carcass while it was still mostly intact.

However, the bite marks are relatively deep (several >4 mm) and numerous, which is unusual for non-tyrannosaur dominated faunas (c.f. Jacobsen 1998), and might indicate the carnivore was trying to remove the last available material from the bone rather than an early stage of carcass consumption. Heavy bite marks are seen on other Morrison specimens but typically in areas unlikely to have contained much flesh (e.g. the distal end of an *Allosaurus* pubic boot – Chure *et al.* 2000). Various
theropods (including both *Allosaurus* and *Ceratosaurus*) have fed upon the remains of Morrison sauropods apparently without leaving bite marks on bones (Jennings & Hasiotis 2006) suggesting that these marks are unusual. Moreover, DINO 5119 is also apparently unique in being the only element from the quarry known with bite marks. Others may potentially be concealed under the shellac coating of older specimens (from the historic period of CQ excavation and now housed in outside institutions) but even so bites would remain very rare. If carcasses in the quarry had been generally accessible to scavengers then far more shed teeth (they are rare in the CQ) and potentially also bite marks would be expected. For example, both Buffetaut and Suteethorn (1989) and Jennings and Hasiotis (2006) found multiple theropod teeth associated with the limbs of sauropod carcasses and inferred these were shed during extensive feeding, despite a lack of bite marks on the bones themselves in either case. However, even if the juvenile diplodocoid had been fed upon prior to transport to the burial site, more marks might be expected on the femur and in particular on its apparent sister element, DINO 5088.

Collectively therefore it is difficult to determine the history of the femur and the traces. However, we suggest this would seem to be a case of opportunistic feeding as opposed to feeding on a kill by the carnivore. The lack of marks on other specimens or other areas of DINO 5119 point to this being an element that for some reason was accessible to a theropod when others were not. The relatively deep bites on the bone suggest an attempt to remove limited flesh (muscle, cartilage, ligaments and tendons) from a bone that had little on it or was incompletely exposed, and point to later stage
carcass consumption, despite the general preference for this region of a limb under normal circumstances. Although far from certain, this hypothesis perhaps best explains the otherwise absence of feeding traces and shed teeth in the quarry.

There are multiple bites on DINO 5119. In addition to the two general sets of bites described above, it is likely that each of these sets may represent more than one single bite by a theropod. Most traces, even those left by very large theropods, consist of a few individual marks and there have a limited separation between them (e.g. Currie & Jacobsen 1995; Chure et al. 2000; Hone & Watabe 2010). If marks A-G do represent a single bite (Figure 3) then there is over 100 mm between A and G and this would mean a total of seven teeth leaving traces, both of which would be highly unusual. Therefore, given the relatively deeper bites of A-D and similar lengths of E-G, it is considered most likely that these subsets are two separate bites, though delivered from a similar position. Similarly, although H is likely confluent with N, there is a group of bites together (M-O) and then several other more distant marks (e.g. I and K) which are unlikely to be part of the same bite. Collectively therefore there are likely four or more individual bites on this bone.

The deeper bites do show that large, non-tyrannosaurid theropods were capable of biting deep into bone, even if this was not a common strategy. Although traces A and B may have been exaggerated by later erosion, both C and D show depths in excess of 4 mm. A number of individual traces are also relatively long (D is 76 mm, and if H and N are one trace, this would be over 100 mm) compared to most recorded for theropods. These long bites do match the feeding style hypothesised for *Allosaurus*
(Snively et al. 2013 - and by extension probably other allosaurs) which were described as long and bird-like pulls. If correct, we might expect most drag marks by larger theropods to be closer to that illustrated in Figure 5A, but the accessibility of a given element or other circumstances might limit this, and other taxa may have favoured alternate strategies.

Although limited, this evidence does suggest that some Morrison theropods were engaging in selective feeding as shown for tyrannosaurines (Hone & Watabe 2010). Heavy bites were directed near the joints with repeated drag marks applied where large areas of muscle may attach. Despite the lack of the tyrannosaur-style premaxillary arcade of proportionally small and specialised D-shaped teeth (Holtz 2004), other large theropods apparently also engaged in similar biting and feeding style. This also matches other known theropod bite traces from the Morrison (e.g. Chure et al. 2000) suggesting this behavior may have been common or even widespread, but merely rarely preserved or not reported.

4. Conclusions

The correct identification of tracemakers is important for making inferences about trophic interactions and behavior based on bite marks. In the absence of shed teeth and with multiple candidates available we note that currently data from tooth spacing and the width of individual traces may be of little value without a better understanding of how different tooth morphologies and possible patterns of feeding
may influence the size and shape of marks. Nevertheless, it appears that at least some
large theropods from the Jurassic did engage in selective feeding patterns comparable
to the later large tyrannosaurs.

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Fig. 1. The juvenile diplodocoid femur DINO 5119 as exposed in-situ in the Carnegie Quarry at Dinosaur National Monument. Scale bar is 10 cm.
Fig. 2. Top: The state of Utah with the location of the Carnegie Quarry indicated by the black dot. Below: stratigraphic column of the Morrison Formation in
Dinosaur National Monument, showing occurrence of the Carnegie Quarry Sandstone. Figure after Turner & Peterson 1999.
Fig. 3. Drawing of DINO 5119 showing the putative bite marks. Putative bite marks are in dark grey and the area of damage to the cortex is in pale grey, a major break in the bone is outlined in black. Letters on the bite marks refer to those described and measured in the text. Scale bar is 100 mm.

Fig. 4. Close up of the head of the femur DINO 5119 (left) and interpretative drawing of the bite marks on it (right) with letters and shading as per Figure 3. Scale bar is 100 mm.
Fig. 5. Illustration of the effects of biting angle and tooth pattern on the spacing between bite marks. Shown is an idealized theropod snout with points representing the tips of the teeth and grey lines, the marks left in a bone or substrate during biting if the head was drawn back. A) Theropod head moves parallel to the long axis of the skull and leaves even spaces between the marks. B) Theropod head moves at a slight angle off parallel leaving narrower spaces between teeth on the left side as seen and wider ones on the right. C) As with B but a still greater angle, exaggerating the differences further. D) Jaws with a missing tooth on the left side as seen, and a misplaced tooth on the right side, causing additional spacing changes.

Table 1. Measurements of the trace marks on DINO 5119 in mm – see Figures 3 and 4 for the identification of each mark.
<table>
<thead>
<tr>
<th>Trace ID</th>
<th>Maximum Length</th>
<th>Maximum Width</th>
<th>Maximum Depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>32</td>
<td>16</td>
<td>18</td>
</tr>
<tr>
<td>B</td>
<td>69</td>
<td>16</td>
<td>12</td>
</tr>
<tr>
<td>C</td>
<td>50</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>D</td>
<td>76</td>
<td>3.5</td>
<td>4.5</td>
</tr>
<tr>
<td>E</td>
<td>48.5</td>
<td>3.5</td>
<td>2</td>
</tr>
<tr>
<td>F</td>
<td>54.5</td>
<td>3.5</td>
<td>1.5</td>
</tr>
<tr>
<td>G</td>
<td>34.5</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>H</td>
<td>56.5</td>
<td>2.5</td>
<td>0.5</td>
</tr>
<tr>
<td>I</td>
<td>12.5</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>J</td>
<td>12</td>
<td>2</td>
<td>0.5</td>
</tr>
<tr>
<td>L</td>
<td>8.5</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>M</td>
<td>18</td>
<td>3</td>
<td>0.5</td>
</tr>
<tr>
<td>N</td>
<td>34</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>O</td>
<td>13.5</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>P</td>
<td>6</td>
<td>0.5</td>
<td>-</td>
</tr>
<tr>
<td>Q</td>
<td>27.5</td>
<td>3</td>
<td>1.5</td>
</tr>
<tr>
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<td>0.5</td>
</tr>
<tr>
<td>R2</td>
<td>9</td>
<td>0.3</td>
<td>&lt;0.5</td>
</tr>
<tr>
<td>R3</td>
<td>6</td>
<td>0.5</td>
<td>&lt;0.5</td>
</tr>
</tbody>
</table>

Note that breaks to the cortex may exaggerate the possible depth of some, especially A and B. Maximum length is measured in a straight line, even when the trace is slightly curved as with D. Although not illustrated as such in Figure 3, trace H is considered to be continuous from trace E to G. Some traces are too shallow to have the depth effectively measured. R has three marks with R1 proximal, and R3 the most distally located.