

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

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

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29 **Keywords:** carnivore-consumed, scavenging, predation, trophic interaction, dinosaur

30

## 31 **1 Introduction**

32

33 Identifying interactions between long extinct non-avian dinosaur (hereafter simply  
34 ‘dinosaurs’) species is a key part of reconstructing trophic levels and foodwebs, and  
35 of the possible structure and function of ancient ecosystems. In addition, this may also  
36 help improve our understanding of the behavior of these animals. However, this is  
37 naturally a difficult prospect – direct evidence is typically limited to bite marks (Hunt  
38 *et al.* 1994), stomach contents (e.g. Charig & Milner 1997) and coprolites (Chin 1997)  
39 - though other sources are occasionally available (e.g. DePalma *et al.* 2013) and it is  
40 often difficult or even impossible to identify even one, let alone both, of the species  
41 involved. All of these sources within the dinosaurian fossil record are rare and  
42 although bite marks are by far the most common of these (e.g. see Jacobsen 1998), it  
43 can be difficult to correctly identify the trace maker when multiple possible  
44 candidates are known.

45 Identification of bites can be best attributed when shed or embedded teeth are  
46 found in association with bite marks (e.g. Currie & Jacobsen 1995; Hone *et al.* 2010;  
47 Xing *et al.* 2012). However, the size and shape of the marks may be indicative in  
48 some circumstances such as in the case of *Tyrannosaurus* (Erickson & Olson; 1996)  
49 where it is the outstanding large carnivore in its environment. Tyrannosaurids produce  
50 a disproportionate number of bite marks on bone compared to other theropods  
51 (Fiorillo 1991; Jacobsen 1998) and represent most of the few theropod bite marks that  
52 have been described in detail. Therefore, new evidence of bite marks from  
53 non-tyrannosaurid dominated faunas are potentially important in assessing the  
54 behavior and ecology of dinosaurs in ecosystems.

55 In marked contrast, bites from non-tyrannosaur dominated faunas are rare (Hone  
56 & Rauhut 2010). Despite the large numbers of specimens from other formations, such  
57 traces remain rare but also little studied. Even in the well-known Morrison beds, only  
58 a limited set of works have looked at bites in detail (e.g. see Matthew 1908, Hunt *et al.*  
59 1994; Carpenter 2000; Carpenter *et al.* 2005; Chure *et al.*, 2000) making any new find  
60 important for understanding non-tyrannosaurian theropods.

61 Here we describe the bite marks from a large and indeterminate theropod on the  
62 femur of a juvenile diplodocoid sauropod in the Carnegie Quarry of the Morrison  
63 Formation (Figure 1). The bites are unusual as this is the only one identified with  
64 theropod bite marks from over 1500 vertebrate elements in the quarry. The nature of  
65 the taphonomy of the preserved femur is unusual but there is some evidence of the  
66 selective feeding strategies also seen in tyrannosaurs. We note that assigning a likely

67 candidate of the tracemaker is especially difficult here. There are numerous large  
68 theropods present in the Carnegie Quarry with likely similar feeding apparatus, and  
69 we show that the size and spacing of bite marks may be difficult to align with  
70 premaxillary arcades.

71

## 72 *1.2 The Morrison Formation*

73 The sediments of the Late Jurassic Morrison Formation are distributed over  $1 \times 10^6$   
74  $\text{km}^2$  across nine states in the Western US (Dodson *et al.* 1980). This formation  
75 represents a mosaic of fluvial, lacustrine (including large hypersaline lakes), and  
76 floodplain environments whose pattern of distribution shifted geographically during  
77 the nearly 7 million years of Morrison deposition. Isotopic dating of  $^{40}\text{Ar}/^{39}\text{Ar}$  from  
78 near the base and high in (although not at the top of) the Morrison yields dates of  
79  $156.84 \pm 0.59$  and  $150.00 \pm 0.52$  Ma respectively (Kowallis *et al.* 1998, as recalibrated  
80 by Trujillo & Kowallis 2015). These dates correspond to a Kimmeridgian through  
81 mid-Tithonian age (Ogg & Hinnov 2012).

82 The Morrison is world renowned for its exceptional paleontological richness of  
83 fossil vertebrates, especially that of dinosaurs (Turner & Peterson 1999; Chure *et al.*  
84 1998, 2006). As a result, it has long attracted the attention of earth scientists and  
85 paleontologists going back into the mid-19<sup>th</sup> century. The formation has been critical  
86 both to our understanding of dinosaur morphology and diversity as well as insight into  
87 Mesozoic terrestrial ecosystems (Ostrom & McIntosh 1966; Foster 2003; Turner &  
88 Peterson 2004). There are numerous large, dinosaur dominated, bones beds that have

89 yielded many tens of thousands of dinosaur fossils, ranging from isolated bones to  
90 spectacularly complete skeletons with skulls. Of these bones beds, the Carnegie  
91 Quarry is unique and a first among equals because of it being the specific resource for  
92 the creation of a national park and its in-situ fossil display.

93

### 94 *1.3 Locality Information*

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

106

### 107 *1.4 The Carnegie Quarry at Dinosaur National Monument*

108 The Carnegie Quarry is situated in the Brushy Basin Member of the Late Jurassic  
109 Morrison Formation in NE Utah, USA (Turner & Peterson 1999). Discovered in 1909  
110 by Earl Douglass of the Carnegie Museum, it is one of the major dinosaur quarries in

111 the Morrison (McIntosh 1977; Dodson *et al.* 1980; McGinnis 1982) and was the  
112 specific site for which Dinosaur National Monument was created in 1915  
113 (Presidential Proclamation 1313). Although extensive excavations took place between  
114 1909 and 1924, the quarry today preserves some 1500 vertebrate bones, exposed  
115 in-situ, in a 60° dipping sandstone bed within the Quarry Exhibit Hall (McIntosh  
116 1977). The CQ is unusual in its tripartite nature, having had many years of excavation  
117 and removal of vast numbers of fossil bones, a very large part of the bone bed with  
118 fossils exposed in-situ and enclosed within a building (Quarry Exhibit Hall), and a  
119 very large part (to the east of that building) exposed on the surface with no  
120 overburden and subjected to little fossil excavation. These three different datasets of  
121 the same bone bed offer many research opportunities.

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

130 Recent recalibration of a previously published  $^{40}\text{Ar}/^{39}\text{Ar}$  isotopic date yields a  
131 value of 150.91 Ma) for a volcanic ash immediately below the quarry sandstone  
132 (Kowallis *et al.* 1998; Trujillo & Kowallis 2015). Balikova (2014) reports a

133 magnetostratigraphic age of Late Tithonian for the quarry sandstone corresponding to  
134 the marine sequence magnetic anomaly subchron CM22n.3n (148.72-148.79 Ma).

135

## 136 **2. Description**

137

138 The bite marks are located on the lateral side of the anterior face of a right femur of  
139 a small sauropod specimen (cataloged as DINO 5119 – Figure 3). Although occurring  
140 in a part of the quarry with many bones, it is not overlapped by any. As a result, DINO  
141 5119 has been completely exposed in anterior view and its full outline is visible. The  
142 element is generally well preserved and in good condition, though, as with many other  
143 bones in the quarry, some of the cortex is damaged and missing from the bone,  
144 including the anterior face of the medial condyle and the anteriomedial part of the  
145 femoral head. There is also a repaired crack across the proximal part of the shaft, but  
146 with no bone loss. The femur is 583 mm long, and 81 mm wide at the narrowest point of  
147 the shaft. The proximal width is 166 mm and the width of the distal end is 183mm.  
148 Approximately 1 m from DINO 5119 there is a left femur of a similarly sized sauropod  
149 (DINO 5088), which almost certainly belongs to the same individual as 5119 based on  
150 their proximity and general similarity of size and form, but this cannot be absolutely  
151 determined.

152 The identity of DINO 5119 is difficult to ascertain, though it is likely a  
153 diplodocoid. The femur is considerably smaller than that of any adult sauropod  
154 identified in the Morrison suggesting it belongs to a young animal. A nearly complete

155 and articulated *Camarasaurus* skeleton from the CQ (CM 11338, Carnegie Museum of  
156 Natural History, Pittsburgh, Pennsylvania, U.S.A.) is only about one-quarter adult size,  
157 and its femoral lengths (550 mm right, 530 mm left) are only slightly less than that of  
158 5119 (Gilmore 1925a). This strongly implies that DINO 5119 is immature (though see  
159 Wedel & Taylor 2013 and Hone *et al.* 2016 on the difficulties of identifying the  
160 ontogenetic status of sauropods). Dwarf sauropod taxa (less than 5 ton adult body  
161 weight) are very rare and associated with island habitats (Sander *et al.* 2006) and not the  
162 center of a continent-sized landmass.

163 The diplodocoids are the most common sauropods in the in the CQ, *Apatosaurus*  
164 *louisae*, *Barosaurus lentus*, and *Diplodocus longus* (Holland 1924; Gilmore 1932,  
165 1936; McIntosh 2005) but the high diversity of the sauropods known from the Morrison  
166 Formation (Farlow *et al.* 2010) means that other credible candidates are also possible, if  
167 less likely. Two features distinguish the femur of Morrison diplodocoids from that of  
168 the macronarian *Camarasaurus*, the only other CQ sauropod. In diplodocoids the  
169 tibial condyle is elongated (Foster, in Wilhite 2005) and the fourth trochanter in  
170 diplodocoids is more proximally placed than in *Camarasaurus*. Unfortunately, these  
171 features are clearly seen only in posterior aspect, an inaccessible view for the in-situ  
172 DINO 5119 and its likely pair 5088. However, close inspection of the exposed medial  
173 edge of the femur in 5119 indicates that the fourth trochanter is on the proximal one  
174 third of the femur, indicating diplodocoid affinities.

175 The femur of an adult *Apatosaurus* is more robust than in adults of *Diplodocus*  
176 and *Barosaurus* (Wilhite 2005). Ontogenetic growth of limb elements in sauropods is



177 isometric so this difference holds for juveniles as well (Tidwell & Wilhite 2005).  
178 DINO 5119 is gracile as in *Diplodocus* and *Barosaurus*. However, the limbs of  
179 *Diplodocus* and *Barosaurus* are difficult to differentiate without associated forelimb  
180 and hindlimb ratios (McIntosh 2005; Wilhite 2005), so given the isolated occurrence  
181 of 5119 we cannot further refine its affinities.

182

### 183 *2.1 Bite marks*

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

194 Alternative origins for the marks beyond bites can be ruled out. DINO 5119 was  
195 exposed in-situ in 1984. Preparation was done with aircsribes and hand tools by  
196 experienced preparators. Of the 1500 bones exposed in-situ in the quarry sandstone  
197 none show gouging preparation tool marks, and even features such as delicate traces of  
198 osteophagus insects have been exposed without damage (Hasiotis *et al.* 1999; Oser &

199 Chure 2016). Hardness of the sandstone varies both across the quarry sandstone and  
200 stratigraphically within it, but separation from the bone is generally good. The  
201 sandstone in the area of DINO 5119 and 5088 is among the most friable in the quarry, to  
202 the extent that it sometimes presents problems of stability that threaten bones with  
203 falling out of the rock. Thus the preparation of DINO 5119 would be easier than in most  
204 other areas of the quarry sandstone. All these facts support our interpretation that the  
205 marks seen on DINO 5119 are tooth traces and not preparation artifacts.

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

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

219 Marks C and D also show fragmentation of the bone towards the dorso-lateral  
220 margin of the bone both more medially show clear drag marks across the surface of

221 the bone. The origins of marks (based on the tapering of the marks away from these  
222 points) for E, F and G lie more medially on the bone than A-D but are mostly shorter  
223 and all are clearly defined.

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

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

236

### 237 **3. Discussion**

238

#### 239 *3.1 Trace maker identity*

240 Although theropods make up a small percentage of the CQ dinosaur fauna, there  
241 are multiple candidates for the bite-maker that known from the quarry. *Allosaurus* is  
242 the most commonly preserved taxon, but *Ceratosaurus* and *Torvosaurus* are also

243 known from limited, but diagnostic, material (Madsen & Welles 2000). Other  
244 theropods from elsewhere in the Morrison Formation (e.g. *Marshosaurus*,  
245 *Ornitholestes*, *Saurophaganax*, *Stokesosaurus* see Weishampel *et al.* 2004) are  
246 currently unknown from the CQ and while they cannot be easily ruled out, are not  
247 considered further here. A crocodyliform – *Goniopholis* – is also known from the  
248 quarry but its relatively low maximum size (jaws typically less than 500 mm in length  
249 – Foster 2006) and the lack of subcircular punctures or splintered surfaces associated  
250 with scores on the bone as seen with modern crocodylian feeding traces (Naju &  
251 Blumenschine 2006; Boyd *et al.* 2013) suggest it is not a credible candidate as the  
252 trace maker and so is not considered further here.

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

261 The premaxillary tooth counts for taxa known in quarry are five per side in  
262 *Allosaurus* (Madsen 1976), and three for *Ceratosaurus* (Madsen & Wells 2000). Britt  
263 (1991) lists the premaxillary tooth count in *Torvosaurus* as “3 (possibly 4)” in the  
264 diagnosis (1991, their page 10). However, in the description Britt gives it as three

265 (1991, their page 13) and his fig. 3E (1991) shows only three. Although only three  
266 alveoli are present, he suggests that a slight depression behind the last alveolus could  
267 be an additional alveolus lost during ontogeny.

268         The maxillary teeth of *Allosaurus* and *Ceratosaurus*, although diagnostic, are  
269 similar for a number of metrics compared to the known variation of theropod teeth  
270 (e.g. see Smith *et al.* 2005) and there are also some similarities in the proportional size  
271 and arrangement of teeth in the skull (Henderson 2000). However, premaxillary teeth  
272 in *Allosaurus* and *Ceratosaurus* differ not only in number but in morphology (Madsen  
273 1976; Madsen & Welles 2000; Britt 1991). Premaxillary tooth crowns in *Allosaurus*  
274 are somewhat D-shaped in cross-section (although the lingual face is slightly convex)  
275 and the crowns are straight. Premaxillary teeth in *Ceratosaurus* are more circular in  
276 cross-section and recurved lingually. The outline of the premaxillary alveoli in  
277 *Torvosaurus* indicates the teeth were more oval in cross section. *Ceratosaurus* differs  
278 from *Allosaurus* and *Torvosaurus* in having several well developed apicobasally  
279 oriented ridges on the lingual face.

280         Premaxillary teeth in these taxa are also different in their orientation in their  
281 respective premaxillae (Britt 1991). In *Ceratosaurus* and *Torvosaurus* the labial side  
282 of each alveolus is overlapped by the alveolus posterior to it, although to a much  
283 greater extent in *Torvosaurus*. *Allosaurus* usually lacks overlap of alveoli but when it  
284 is present it is small the alveolus overlaps the lingual side of the next posterior  
285 alveolus. These differences may well reflect different feeding strategies and might, in  
286 the future, prove useful or even diagnostic for identifying the tooth trace makers.

287 However, that will require more detailed formal descriptions and comparisons first.

288       There are several known deep bites into or through bones (Hunt *et al.* 1994;,  
289 Chure *et al.* 2000; Carpenter 2005) preserved in the Morrison Formation that can be  
290 attributed to large-bodied theropods. These include bites in excess of 5 mm in depth  
291 (Chure *et al.* 2000), and although the exact size and identity of the animals that  
292 inflicted these marks is unknown, it is clear that at least some locally present  
293 theropods could produce bites deeper than those seen here on DINO 5119. Rayfield  
294 (2005) examined the possible mechanics of biting in *Allosaurus* and showed that it  
295 was less well suited to leaving bites than large tyrannosaurines. However, this does  
296 not rule out biting through bones, and in the absence of comparative studies of other  
297 Morrison theropods this is sadly uninformative as to the possible identity or otherwise  
298 of the trace maker. Similarly, Snively *et al.* (2013) suggested *Allosaurus* was well  
299 adapted to produce a bird-like ‘posterior pull’ feeding style which may fit with the  
300 long scrape marks here but does not necessarily rule out other candidates. Collectively  
301 therefore, bite depth and shape provides no definitive information to assist in  
302 identifying a possible trace maker.

303       The relative width of individual marks that should reflect the width of a single  
304 tooth that produced them, is also of limited value. Although *Allosaurus*, *Torvosaurus*  
305 and *Ceratosaurus* are homodont (at least compared to derived tyrannosaurs e.g. see  
306 Smith *et al.* 2005), they would have had different sized teeth in the jaws of individuals,  
307 and animals of different sizes would have different sized teeth relative to other  
308 conspecifics. The width of a single trace could potentially be used to determine the

309 size of the tooth that made the mark, but overlapping sizes and issues such of degrees  
310 of wear on the tooth crown could also affect the size of a given tooth (the angle of use  
311 could be a still greater issue, see below). In any case, although the teeth of these three  
312 theropods do differ in terms of details such as degree of curvature and denticle counts,  
313 there is currently no known relationship of this to trace shapes. The gross morphology  
314 of the teeth (laterally compressed and recurved) is similar in all three taxa.

315 Finally, the spacing between individual tooth marks and their apparent size in  
316 combination may give an indication at least of the size of an individual trace marker.  
317 However, again there are potential complications here. Although some putative  
318 theropod bite marks show the teeth moved in arcs across the face of a bitten bone (e.g.  
319 Hone *et al.* 2010 c.f. feeding traces of some extant reptiles – D’Amore &  
320 Blumenschine 2009, 2012) the vast majority seem to be simple straight ‘pulls’. These  
321 actions leave straight lines, or sets of sub-parallel lines (e.g. Hunt *et al.* 1994; Currie  
322 & Jacobsen 1995; Jacobsen 1998; Rogers *et al.* 2003; Hone & Watabe 2010) as traces,  
323 such as seen here. This latter biting style should place the minimum amount of stress  
324 on typical theropod teeth (at least the maxillary and dentary teeth) as it would align  
325 the stress with the long axis of the cross-section of the tooth. However, even  
326 thin-toothed reptiles apparently use the ‘medial-caudal arc’ feeding strategy when  
327 teeth are contacting bone, (D’Amore & Blumenschine 2009) suggesting that this was  
328 not necessarily a limitation of theropod feeding with tooth-bone contact. Even so, the  
329 rarity of bites from non-tyrannosaurian theropods suggests that these animals often  
330 avoided tooth-bone contact (Hone & Rauhut 2010).

331 Even if the jaws were moving such that the stress was delivered close to parallel  
332 to this axis of the tooth, small changes in the angle at which this is delivered could  
333 change the spacing between individual marks (Figure 5), and more dramatic changes  
334 in angle could leave very closely spaced marks for even widely spaced teeth. The  
335 spaces between individual scrapes might therefore be considered a useful minimum  
336 for tooth spacing, but multiple overlapping bites by one animal may occur (e.g. Hone  
337 & Watabe 2010) and it is likely difficult or impossible to tell one bite from multiple  
338 bites when only a small number of traces are seen as with DINO 5119. The three  
339 subparallel scrapes could represent one bite of three teeth, one of two teeth and one  
340 bite of one tooth, or one tooth applied three separate times.

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

349 Similarly, bites delivered at an angle (e.g. Figure 5A vs 5C) could affect the width  
350 of individual traces. Even at the tip, the teeth of large Jurassic theropods are broader  
351 on their lateral than posterior faces. Thus a drag mark produced by the same tooth  
352 drawn at an angle would produce a wider trace than one drawn directly backwards.



353 Therefore, the breadth of a drag mark may not be a good indicator of tooth size, and  
354 fracturing of the cortex or erosion may further change the shape.

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

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

372

### 373 *3.2 Behaviour*

374 Determining the difference between scavenging and a predatory event is difficult

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

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

391 However, the bite marks are relatively deep (several >4 mm) and numerous,  
392 which is unusual for non-tyrannosaur dominated faunas (c.f. Jacobsen 1998), and  
393 might indicate the carnivore was trying to remove the last available material from the  
394 bone rather than an early stage of carcass consumption. Heavy bite marks are seen on  
395 other Morrison specimens but typically in areas unlikely to have contained much flesh  
396 (e.g. the distal end of an *Allosaurus* pubic boot – Chure *et al.* 2000). Various

397 theropods (including both *Allosaurus* and *Ceratosaurus*) have fed upon the remains of  
398 Morrison sauropods apparently without leaving bite marks on bones (Jennings &  
399 Hasiotis 2006) suggesting that these marks are unusual.

400       Moreover, DINO 5119 is also apparently unique in being the only element from  
401 the quarry known with bite marks. Others may potentially be concealed under the  
402 shellac coating of older specimens (from the historic period of CQ excavation and  
403 now housed in outside institutions) but even so bites would remain very rare. If  
404 carcasses in the quarry had been generally accessible to scavengers then far more shed  
405 teeth (they are rare in the CQ) and potentially also bite marks would be expected. For  
406 example, both Buffetaut and Suteethorn (1989) and Jennings and Hasiotis (2006)  
407 found multiple theropod teeth associated with the limbs of sauropod carcasses and  
408 inferred these were shed during extensive feeding, despite a lack of bite marks on the  
409 bones themselves in either case. However, even if the juvenile diplodocoid had been  
410 fed upon prior to transport to the burial site, more marks might be expected on the  
411 femur and in particular on its apparent sister element, DINO 5088.

412       Collectively therefore it is difficult to determine the history of the femur and the  
413 traces. However, we suggest this would seem to be a case of opportune feeding as  
414 opposed to feeding on a kill by the carnivore. The lack of marks on other specimens  
415 or other areas of DINO 5119 point to this being an element that for some reason was  
416 accessible to a theropod when others were not. The relatively deep bites on the bone  
417 suggest an attempt to remove limited flesh (muscle, cartilage, ligaments and tendons)  
418 from a bone that had little on it or was incompletely exposed, and point to later stage

419 carcass consumption, despite the general preference for this region of a limb under  
420 normal circumstances. Although far from certain, this hypothesis perhaps best  
421 explains the otherwise absence of feeding traces and shed teeth in the quarry.

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

435       The deeper bites do show that large, non-tyrannosaurid theropods were capable of  
436 biting deep into bone, even if this was not a common strategy. Although traces A and  
437 B may have been exaggerated by later erosion, both C and D show depths in excess of  
438 4 mm. A number of individual traces are also relatively long (D is 76 mm, and if H  
439 and N are one trace, this would be over 100 mm) compared to most recorded for  
440 theropods. These long bites do match the feeding style hypothesised for *Allosaurus*

441 (Snively *et al.* 2013 - and by extension probably other allosaurs) which were  
442 described as long and bird-like pulls. If correct, we might expect most drag marks by  
443 larger theropods to be closer to that illustrated in Figure 5A, but the accessibility of a  
444 given element or other circumstances might limit this, and other taxa may have  
445 favoured alternate strategies.

446       Although limited, this evidence does suggest that some Morrison theropods were  
447 engaging in selective feeding as shown for tyrannosaurines (Hone & Watabe 2010).  
448 Heavy bites were directed near the joints with repeated drag marks applied where  
449 large areas of muscle may attach. Despite the lack of the tyrannosaur-style  
450 premaxillary arcade of proportionally small and specialised D-shaped teeth (Holtz  
451 2004), other large theropods apparently also engaged in similar biting and feeding  
452 style. This also matches other known theropod bite traces from the Morrison (e.g.  
453 Chure *et al.* 2000) suggesting this behavior may have been common or even  
454 widespread, but merely rarely preserved or not reported.

455

#### 456 **4. Conclusions**

457

458       The correct identification of tracemakers is important for making inferences  
459 about trophic interactions and behavior based on bite marks. In the absence of shed  
460 teeth and with multiple candidates available we note that currently data from tooth  
461 spacing and the width of individual traces may be of little value without a better  
462 understanding of how different tooth morphologies and possible patterns of feeding

463 may influence the size and shape of marks. Nevertheless, it appears that at least some  
464 large theropods from the Jurassic did engage in selective feeding patterns comparable  
465 to the later large tyrannosaurs.

466

467

#### 468 **Acknowledgments**

469 *We thank Brooks Britt and Tom Holtz for discussion of the specimen, and Ray Wilhite*  
470 *and Matt Bonnan for helpful discussions about the affinities of 5119. Thanks to Colm*  
471 *Bane for assistance in photographing DINO 5119 on the quarry face. We also thank*  
472 *two anonymous referees for comments which helped to improve the manuscript.*

473

474

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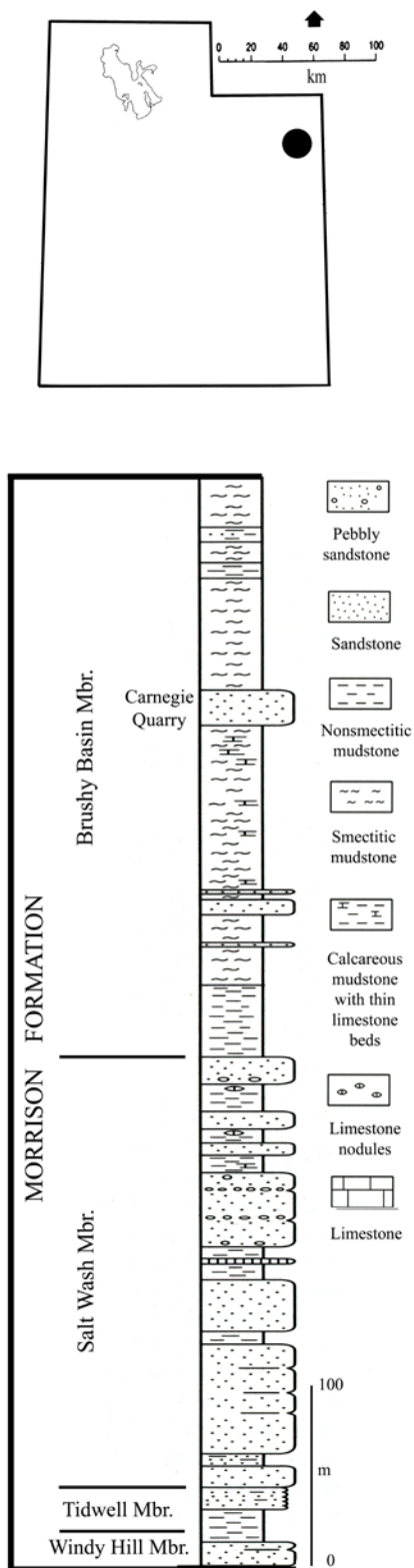
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702 *Fig. 1.* The juvenile diplodocoid femur DINO 5119 as exposed in-situ in the Carnegie

703 Quarry at Dinosaur National Monument. Scale bar is 10 cm.

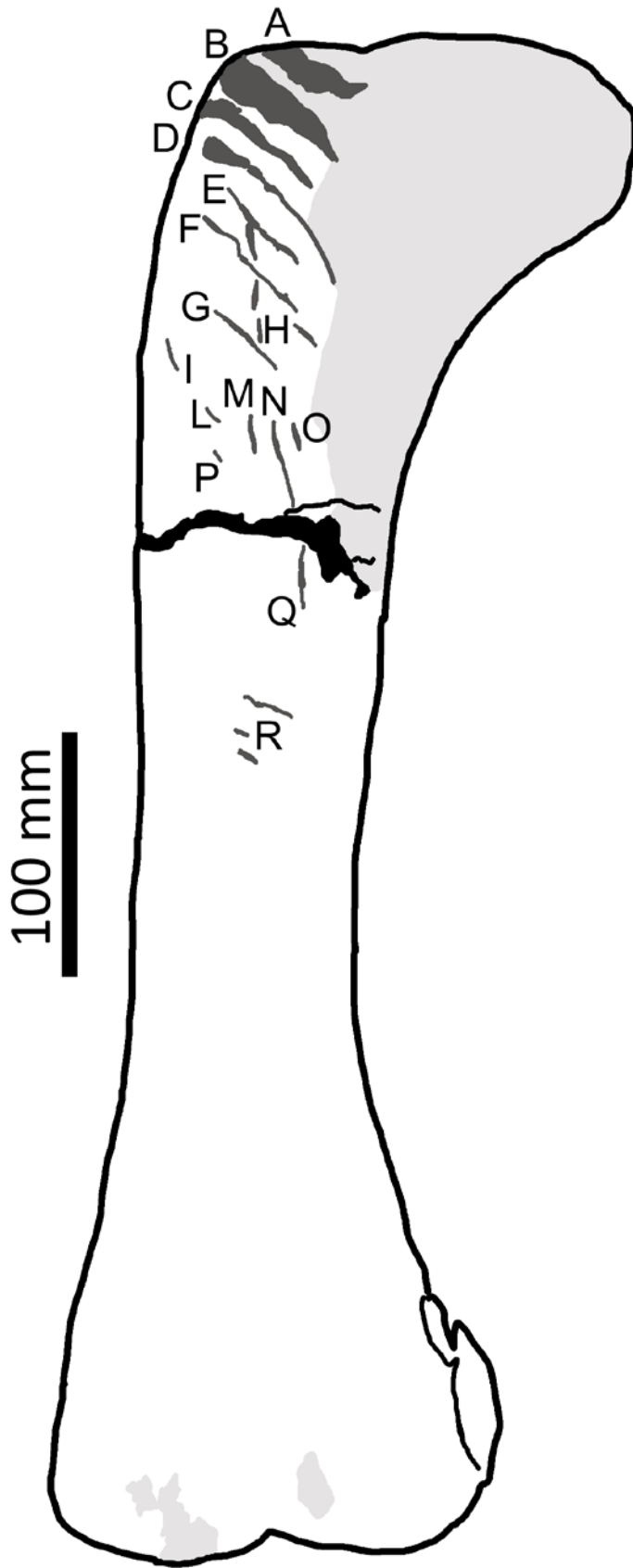


704

705 *Fig. 2.* Top: The state of Utah with the location of the Carnegie Quarry indicated by

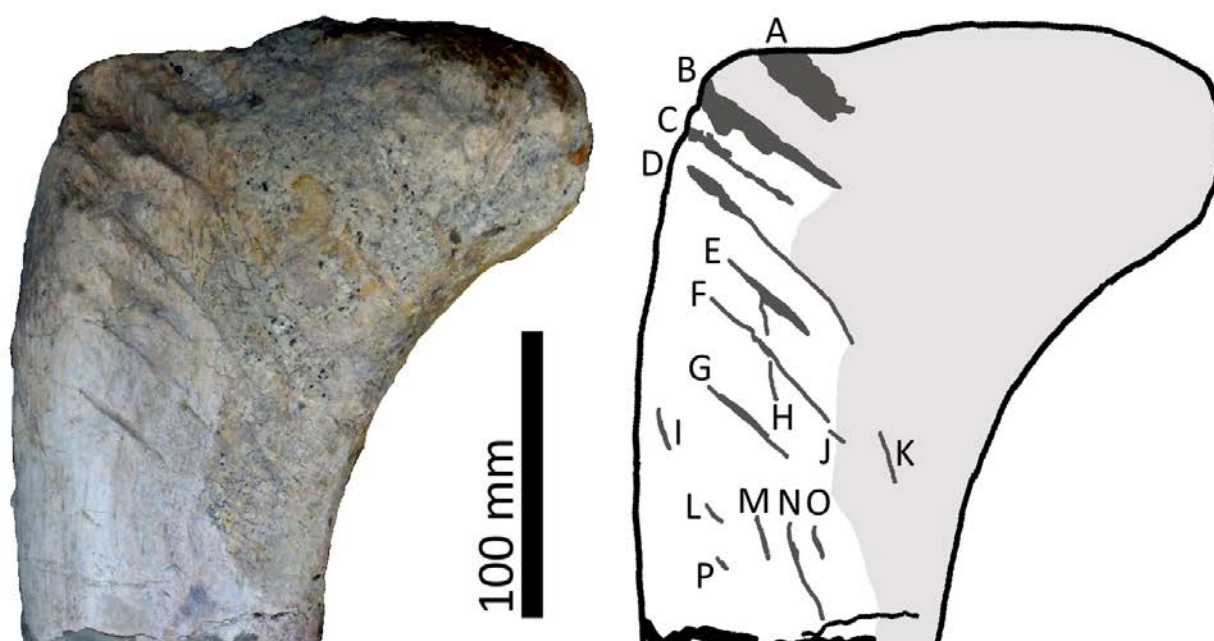
706 the black dot. Below: stratigraphic column of the Morrison Formation in

707 Dinosaur National Monument, showing occurrence of the Carnegie Quarry  
708 Sandstone. Figure after Turner & Peterson 1999.  
709



711 *Fig. 3.* Drawing of DINO 5119 showing the putative bite marks. Putative bite marks  
 712 are in dark grey and the area of damage to the cortex is in pale grey, a major  
 713 break in the bone is outlined in black. Letters on the bite marks refer to those  
 714 described and measured in the text. Scale bar is 100 mm.

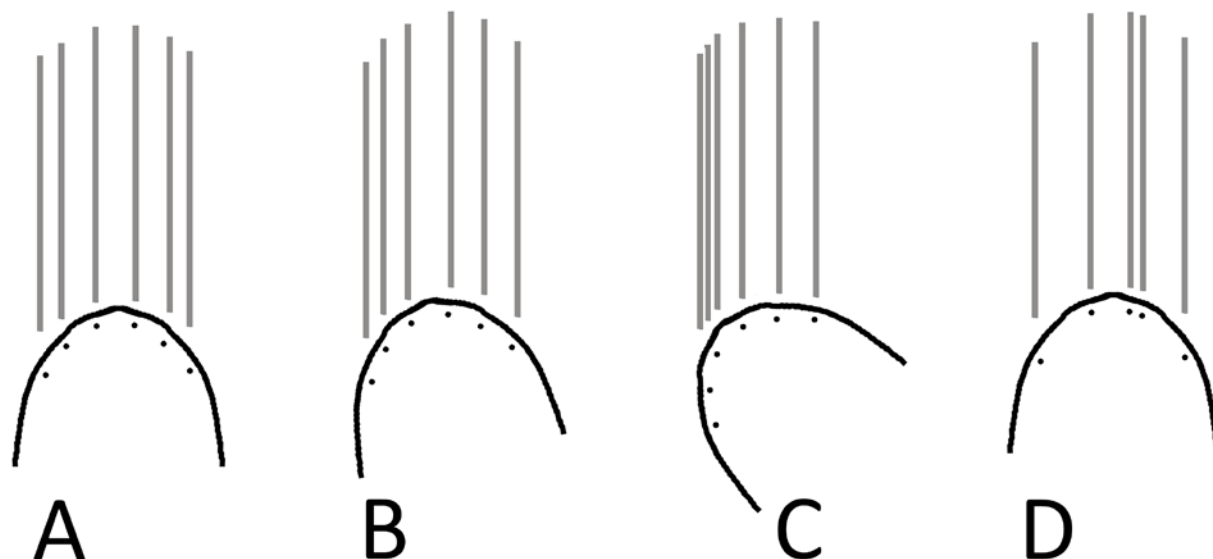
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717 *Fig. 4.* Close up of the head of the femur DINO 5119 (left) and interpretative drawing  
 718 of the bite marks on it (right) with letters and shading as per Figure 3. Scale  
 719 bar is 100 mm.

720



721

722 *Fig. 5.* Illustration of the effects of biting angle and tooth pattern on the spacing  
 723 between bite marks. Shown is an idealized theropod snout with points  
 724 representing the tips of the teeth and grey lines, the marks left in a bone or  
 725 substrate during biting if the head was drawn back. A) Theropod head moves  
 726 parallel to the long axis of the skull and leaves even spaces between the  
 727 marks. B) Theropod head moves at a slight angle off parallel leaving  
 728 narrower spaces between teeth on the left side as seen and wider ones on the  
 729 right. C) As with B but a still greater angle, exaggerating the differences  
 730 further. D) Jaws with a missing tooth on the left side as seen, and a misplaced  
 731 tooth on the right side, causing additional spacing changes.

732

733

734 *Table 1.* Measurements of the trace marks on DINO 5119 in mm – see Figures 3 and 4

735 for the identification of each mark.

736

Trace ID	Maximum Length	Maximum Width	Maximum Depth
A	32	16	18
B	69	16	12
C	50	4	4
D	76	3.5	4.5
E	48.5	3.5	2
F	54.5	3.5	1.5
G	34.5	2	1
H	56.5	2.5	0.5
I	12.5	1	-
J	12	2	0.5
L	8.5	1	-
M	18	3	0.5
N	34	2	1
O	13.5	3	1
P	6	0.5	-
Q	27.5	3	1.5
R1	22	1.5	0.5
R2	9	0.3	<0.5
R3	6	0.5	<0.5

737

738 Note that breaks to the cortex may exaggerate the possible depth of some, especially

739 A and B. Maximum length is measured in a straight line, even when the trace is

740 slightly curved as with D. Although not illustrated as such in Figure 3, trace H is

741 considered to be continuous from trace E to G. Some traces are too shallow to have

742 the depth effectively measured. R has three marks with R1 proximal, and R3 the most

743 distally located.

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