Pre- and postmortem tyrannosaurid bite marks on the remains of Daspletosaurus (Tyrannosaurinae: Theropoda) from Dinosaur Provincial Park, Alberta, Canada

David Hone, Darren H Tanke

Trace marks on the bones of non-avian dinosaurs may relate to feeding by large carnivorans or as a result of combat. Here the cranium and mandible of a specimen of Daspletosaurus are described that show numerous pre-mortem injuries with evidence of healing and these are inferred to relate primarily to intraspecific combat. In addition, post-mortem damage to the jaw and teeth and part of the skull are indicative of late stage carcass consumption and taphonomic context suggest that this was scavenging. These post-mortem bites were delivered by a large bodied tyrannosaurid theropod and may have been a second Daspletosaurus, and thus this would be an additional record of tyrannosaurid cannibalism.

1   **Pre- and postmortem tyrannosaurid bite marks on the remains of**

2   ***Daspletosaurus* (Tyrannosaurinae: Theropoda) from Dinosaur Provincial**

3   **Park, Alberta, Canada**

4

5   *Hone, D.W.E.[1] & Tanke, D.H.[2]

6

7   1. School of Biological and Chemical Sciences, Queen Mary, University of London, Mile End

8   Road, London, E1 4NS, U.K.

9

10   2. Royal Tyrrell Museum, Box 7500, Drumheller, Alberta, T0J 0Y0, Canada.

11

12   *Corresponding author: dwe_hone@yahoo.com

13

14

15

16   **Abstract:**

17   Trace marks on the bones of non-avian dinosaurs may relate to feeding by large carnivorans

18   or as a result of combat. Here the cranium and mandible of a specimen of *Daspletosaurus* are

19   described that show numerous pre-mortem injuries with evidence of healing and these are

20   inferred to relate primarily to intraspecific combat. In addition, post-mortem damage to the jaw

21   and teeth and part of the skull are indicative of late stage carcass consumption and taphonomic

22   context suggest that this was scavenging. These post-mortem bites were delivered by a large

23   bodied tyrannosaurid theropod and may have been a second *Daspletosaurus*, and thus this would

24   be an additional record of tyrannosaurid cannibalism.

25

26

27   **Keywords:** feeding traces, scavenging, tyrannosaur, palaeoecology

28

29

30   **Introduction:**

31   Evidence of carnivore-consumed interactions in the fossil record are important for

32   reconstructing the ecology, and determining trophic interactions, of extinct taxa. Much research

33   has investigated the diet and putative behaviours of the carnivorous members of the theropod

34   clade of non-avian dinosaurs (hereafter simply 'dinosaurs') examining how prey may have been

35   acquired (Rayfield, 2005), handled (Fowler et al., 2011) and consumed (Erickson & Olson,

36   1996), and what prey was targeted (Hone & Rauhut, 2010). Theropods had a diverse diet

37   including fish (Charig & Milner, 1997), mammals (Larson et al., 2010), lizards (Ostrom, 1978),

38   pterosaurs (Hone et al., 2012), other non-avian dinosaurs (Varricchio, 2001) and birds (O'Connor

39   et al., 2011) and evidence suggests at least some theropods were both predators and scavengers,

40   and in particular, large tyrannosaurs were both predators and scavengers (Holtz, 2008; Hone &

41   Watabe, 2010).

42   Three main lines of evidence are typically used to show tropic interactions between

43   carnivorous theropods and consumed taxa: gut contents of ingested bones or other elements, bite

44   marks on material that was not ingested, and coprolites of formerly consumed material. Both

45   stomach contents and coprolites for theropod dinosaurs are extremely rare (Chin, 1997), but even

46   bite marks are uncommon (though in part likely to be under recorded). Note that here we use the

47   term "carnivore-consumed" as opposed to the more common "predator-prey" as the latter make

48   an implicit statement that the consumed animal was actively hunted and killed, and thus is

49   inappropriate for referring to scavenged food items, or where the status is not known. Therefore

50   "predator-prey" should be restricted in use to instances where it can be determined that prey was

51   actively killed by the consuming carnivore in question.

52   Theropods may have generally fed carefully and avoided tooth-on-bone contact (Hone &

53   Rauht, 2010), but tyrannosaurs with their powerful bites (Rayfield, 2004) may have been

54   exceptions (Hone & Rauhut, 2010). Certainly, they were capable of both huge and powerful bites

55   into bone (Erickson & Olson, 1996) but also were selective feeders, adjusting biting style to the

56   material at hand and the intended results (Hone & Watabe, 2010). Even so, overall tyrannosaurs

57   seem to have produced more bite marks than other theropods (Jacobsen, 1998) suggesting that

58   their feeding strategy involved greater tolerances of tooth-bone contact and / or actual deliberate

59   biting of, and potentially consumption of, bones.

60   Increasing numbers of theropod-theropod carnivorous interactions are known (e.g.

61   *Sinocalliopteryx* – Xing et al., 2012; *Tyrannosaurus* – Longrich et al., 2010) and while likely

62   relatively rare (if only because carnivores are much less common in macroscopic terrestrial

63   ecosystems than are herbivores) show that theropods did consume, and probably on occasion

64   actively killed for food, other carnivores. However, bites or injuries to theropods may not be the

65   result of attempted predation alone. Some large theropods engaged in cranio-facial biting (Tanke

66   & Currie, 1998; Bell & Currie, 2010), presumably at least in part being some form of ritualized

67   combat linked to socio-sexual dominance contests and combat may also have involved wounds

68   inflicted by the feet (Rothschild, 2013). Healed bites on the crania of large theropods show

69   evidence of combat with other large theropods, and these are not normally matched with injuries

70   elsewhere (which are comparatively uncommon) on the body of the animals suggesting it was not

71   a predation attempt (cf damage distal parts of the axial series when predation was attempted:

72   Carpenter, 2000; DePalma et al., 2013). This adds to the complexity of correctly determining

73   interactions between two large carnivores from potential predation / consumption of one by

74   another.

75   Here we document the remains of a large tyrannosaurine theropod, *Daspletosaurus* sp., from

76   Alberta, Canada, that shows evidence of numerous healed injuries to the cranium and mandible

77   inflicted by another large theropod, probably a tyrannosaurid. Additional bite marks inflicted on

78   the lower jaw appear to be post mortem and are attributed to another tyrannosaurid, and evidence

79   for the decay and disarticulation of the material at the time these marks were inflicted suggests

80   this was a scavenging event.

81

82   **Institutional Abbreviations:** TMP, Tyrrell Museum of Palaeontology, Alberta, Canada.

83

84   **Locality Information:**

85   The specimen was originally discovered by P.J. Currie in the 1994 field season and was

86   excavated from Quarry 215, Dinosaur Provincial Park, (L0315) over several summers. The

87   specimen is from the lower part of the Dinosaur Park Formation.

88   Despite disarticulation it can be seen from the general pattern of mapped bones that the

89   carcass arrived on site more or less intact (distal tail to tip of snout, ribs, pelvis), laying on its

90   right side in opistotonic posture, and then decayed and the elements came apart in place. The

91   position of the mapped bones vs. the edge of the quarry suggests that is quite possible that the

92   major fore- and hindlimb elements were present but eroded, though no eroded limb bone pieces

93   were found aside from part of one femur. Erosion rates and postulated position of the limbs

94   suggests that if this occurred it was many years before the discovery of the specimen.

95

96   **Attribution to *Daspletosaurus*:**

97   Identifying TMP 1994.143.0001 as *Daspletosaurus* is not straight forwards. Currie (2003)

98   described this material as a juvenile of *Daspletosaurus*, but did not any reason for this assignment

99   (though he noted much in common with confirmed specimens of this genus). Holtz (2004) noted

100   that *Daspletosaurus* could be diagnosed by a convex tab-like process on the postorbital, an

101   element not preserved here. Some of the diagnostic characteristics originally given by Russell

102   (1970) are problematic or no longer diagnostic for the genus (e.g. "maxillary teeth large, not

103   greatly reduced posteriorly") although others are present here (e.g. premaxilla doe s not contact

104   nasal below external naris). The specimen appears to have 18 dentary alveoli, one higher than is

105   normal for *Daspletosaurus*, but also higher than any other tyrannosaurid (except occasional

106   specimens of *Albertosaurus* – Carr and Williamson, 2000) supporting this assignment.

107   Furthermore, Carr and Williamson (2004) noted that *Daspletosaurus* is unusual for a

108   tyrannosaurid in having the tooth denticles of the mesial carinae reach the base of the tooth, a

109   feature seen here. Coding of the analysis by Brusatte et al. (2010) also suggests that the maxillary

110   fenestra, location abutting the ventral margin of the antorbital fossa is diagnostic for this genus

111   compared to other tyrannosaurines (their character 18) and this is apparently present here

112   although there is a slight space between the two margins. Collectively however, despite the issues

113   described above, this specimen can be confidently assigned to this genus.

114

115   **Preservation of material:**

116   The specimen (TMP 1994.143.0001) is mostly very well preserved, with superb surface

117   texture and fine details preserved. However, there is a great deal of cracking on the cortex of

118   many elements (and especially on the skull) and some pieces show some heavy damage (e.g. the

119   partial femur). There appears to be little distortion to the preserved bones, even in relatively thin

120   and fragile skull elements, though the major skull piece does seem to have been sheared

121   somewhat. The bones are a rich brown colour and lie within a grey-green coloured silty matrix

122   with small clayballs.

123   Some pieces of the carcass were still articulated when discovered (e.g. the dorsals and some

124   dorsal ribs) indicating a lack of transport damage, and there is no evidence of fluvial action (e.g.

125 abrasions to bone surfaces). The overall condition of the material suggests that it was buried in

126 situ in the fine-grained siltstones. This is further supported by the lack of wide scattering of

127 elements, and the lack of alignment of long-axis orientations of bones. Fragile elements such as

128 the gastralia and parts of the braincase parts have survived intact despite some movement in the

129 quarry while the breakage of the supradentary was recent in origin. The skeleton is rather

130 incomplete (see below) however the evidence for recent erosion suggests that more material may

131 have been lost prior to its discovery and excavation. There is some stratification of elements of

132 the tyrannosaur within the quarry, with pieces lying over each other by separated by sediment

133 suggesting possible transport or the movement of elements by other agents (e.g. scavengers).

134 Elements of vertebrates that do not belong to the *Daspletosaurus* were also recovered from

135 the quarry. This includes a tibia and phalanx of small theropod, a very incomplete hadrosaur

136 femur, ornithischian teeth, crocodilian teeth and a single osteoderm and finally a piece of turtle

137 plastron. All are typical components of the Dinosaur Park fauna and occur regularly in the

138 quarries (Eberth & Currie, 2005).

139

140 **Description:**

141 The specimen TMP 1994.143.0001 is that of an immature individual of *Daspletosaurus* sp., a

142 large tyrannosaurine theropod. The animal is represented by a mostly complete, but

143 disarticulated, skull and partial post cranium. Most of the skull material has previously been

144 illustrated (Currie, 2003), and much work has been done on tyrannosaurine cranial morphology

145 and ontogeny and taxonomic implications (e.g. Brochu, 2003; Hurum & Sabath, 2003; Carr &

146 Williamson, 2004; Hone et al., 2012), and so the material will not be redescribed here, and

147 instead we limit ourselves to comments on the elements of interest and damage or marks to them.

148 A large piece of the skull consisting front and right part of the cranium is represented by the

149 premaxillae, maxillae, nasals and the right jugal and lacrimal. On the right side, the cranium is

150   intact as far as the orbit (Fig. 1), and the left side is complete as far as the anterior part of the

151   antorbital fenestra (Fig. 2). This part of the cranium as preserved totals 550 mm in length.

152   Numerous other cranial and mandibular elements are also preserved including fragile and / or

153   rarely preserved elements such as the braincase, supradentary, ectopterygoids, surangular, and

154   palatines. There are alevoli for three premaxillary teeth and 13 maxillary teeth. All of these 16

155   teeth are preserved in the right side of the skull with just 6 on the left, with others being missing.

156   There may have been more originally in the maxilla, but the posterior part on right is broken. The

157   largest maxillary teeth have a crown height of just over 50 mm.

158   The main piece of the cranium is slightly distorted showing shearing along the midline of the

159   skull, and elements have shifted and separated slightly along the sutures. Numerous foramina are

160   present on the premaxilla, along the ventral margin of the maxilla and along the nasals. The

161   nasals are especially rugose and show peaks and pits across their surface.

162   The right dentary is nearly complete with nine preserved teeth plus one emerging

163   replacement crown with a total of 18 dental alveoli. The dentary teeth are displaced from jaws

164   and do not mostly lie in their respective alveoli. The total length of the mandible as preserved 380

165   mm. There is no sign of left dentary, but this must have originally been present based on the

166   number of isolated teeth recovered (see discussion for details).

167   At least parts of most major areas of the post cranial skeleton are preserved including

168   cervical vertebrae, dorsal vertebrae, dorsal ribs and gastralia, caudal vertebrae and chevrons (the

169   caudals vertebrae and chevrons are in especially good condition), a partial ilium and partial

170   femur. Most however have suffered some damage and are incomplete, with severe damage to

171   some elements (e.g. the femur).

172   The specimen is considered to be non-adult animal based on the separation of some elements

173   suggesting they were not fully fused, and also the overall size of the animal. For example an adult

174   specimen of *Daspletosaurus* have frontals of around 145 mm compared to just 99 mm here (data

175 from Currie, 2003). Similarly, Aldult specimens have a dentary tooth row of 430-455 mm

176 (Currie, 2003) compared to that of TMP 1994.143.0001 which is only 290 mm. Currie (2003)

177 estimated the total length of TMP 1994.143.0001 as a whole animals at 5.8 m based on the size of

178 the preserved parts of the skull.

179

180 **Bite marks and breaks:**

181 Every available element and fragment of bone (which totalled over a hundred pieces) was

182 examined closely for bite marks or traces of damage. All damage that could be identified as being

183 of Cretaceous in age, rather than more recent breaks or erosion, was restricted to the cranial and

184 mandibular elements with the exception of a healed break on a dorsal rib. There is also no

185 indication of bite-mark like damage to any other vertebrate material in the quarry. Both damage

186 that was premortem and postmortem could be identified, in addition to some of indeterminate

187 origin.

188

189 *Premortem:*

190 The vast majority of the identified marks on the skull are premortem, indicating that

191 numerous injuries or infections occurred at various times in the life of the individual. These must

192 also have occurred prior to death at such a time as to allow for evidence for healing and repair to

193 be visible. Premortem bites and damage are considered as such based on evidence of healing

194 through pathology, or presence of finely pitted reactive bone and also anomalous directions of

195 pits combined with raised ridge (Rothschild & Martin, 1993; Tanke & Rothschild, 2002).

196

197 A. A bite on the tip of the snout with bulged and pathological area on the right ascending process

198 of the premaxilla and apparent fusion of the right and left premaxillary processes (Figs 1-3). This

199 damage is associated with a small subcircular mark approximately 13 mm in diameter, and 6 mm

200   in depth, on the anteriolateral face of the left premaxilla. A second suboval (16 mm long by 6 mm

201   across, and less than 2 mm deep) mark lies 6 mm posteriorly to this at the juncture of the right

202   premaxilla and right nasal. The long axis of the oval is subparallel to the ramus of the

203   premaxillary process.

204

205   B. A lesion which is close in form to a bite-and-drag mark (anterior to dorsally directed) on the

206   anteriolateral part of left maxilla (Fig 2). This is 22 mm long by 8 mm (widest point) and max

207   depth in puncture of 1.5 mm. It is a distinctly different colour to of surrounding bone being more

208   of a burnt-orange than brown.

209

210   C. Comma-shaped damage anterioventral to the promaxillary fenestra on the right maxilla (Fig

211   2). This is 22.5 mm long, 6.5 mm wide at the top and 1.5 mm wide at base. It appears to be a

212   bone avulsion that was torn out, and is recessed in the excavation of the maxilla. There is

213   evidence of healing on the maxilla around the edges of this damage, but not apparently on the

214   avulsion. This is close in appearance to some tyrannosaurine bite-and-drag marks (sensu Hone &

215   Watabe, 2010), and here is anterioventrally directed.

216

217   D. A serious of legions and injuries on the right maxilla (Fig 1). Two very small lesions on the

218   right maxilla that lie on the posteriorly directed ramus, below the right nasal. The first is of mild

219   osteomyelitis and tracks the upper margin of the right promaxillary fenestra (Fig 4). This is a

220   small subcircular lesion, 7 mm long and 6 mm tall and 2 mm deep. The second lies in line with

221   the long axis of the left naris, and is a large and subcircular lesion measuring 15 mm in diameter

222   and with a maximum depth of 2 mm. This lies alongside the edge of the maxilla, but does not

223   extend onto the other element.

224   Just dorsal to the 7th maxillary alveolus is a groove that is posterio-ventrally directed, it is

225   16.5 mm long is up to 6.5 mm wide and 2 mm deep (Fig). Similarly, on the ventral margin of

226   maxilla above 9th alveolus is a dorsoventrally directed notch 11 mm tall, 4 mm in width and up to

227   2.75 mm deep.

228   A pair of conjoined subcircular depressions are apparent on the anteriordorsal edge of the

229   right maxilla, close to the suture with the right premaxilla. A major lesion lies on the anterior part

230   of the right maxilla, represented by a moderately thickened patch (slightly raised by 1 or 2 mm

231   compared to the surrounding bone) of reactive bone suggestive of osteomyelitis. This area

232   measures 48.5 mm tall, and is up to 31 mm wide.

233

234   E. A large sub-circular puncture (9 mm across, approx 2 mm deep) lies in the dorsal part of the

235   middle of the left nasal (Fig 3). The right nasal also has small lesion just dorsal to the

236   dorsoposterior edge of the narial opening, it is 10 mm long by 5 mm. A second lesion occurs on

237   the right side of the right nasal where it contacts the maxilla, 30 mm posterior to the posterior

238   most part of the right naris (Fig 1, 2). This lesion is subcircular and 14 mm in diameter, and

239   around 1 mm in depth. It is composed of darker bone colour than the surrounding tissue and is

240   finely pitted both inside the lesion and also around the margin of it. There are two slightly raised

241   irregularly shaped 'islands' of bone that sit within the lesion, these are prominent and have a

242   smoother texture than the other pitted bone.

243

244   F. A lesion on the right jugal that penetrates the bone fully (Fig 1). A semicircular area (which is

245   estimated at 11 mm tall and approx 7 mm across based on the lack of a posterior part) has been

246   removed from the element. Mildly reactive bone is present around the edge of this, increasing the

247   overall length of the damage to 24 mm by 14.75 mm, with an anteriorly a swollen area showing

248   evidence of osteomyelitis. A small premortem lesion, ventral to the above described one, is also

249   present and measures 11 mm long by 8.5 mm tall.

250

251   G. A pit on the left lacrimal is 6.5 mm across and 3 mm deep. See also below.

252

253   H. A posteriorly directed lesion, that includes a pit in the anterior part, that lies on the left

254   posterior edge of the postorbital descending process, just above the tip of the ascending process

255   of the left jugal (Fig 6). The lesion is 2 mm deep, 13 mm long and 5 mm wide and shows signs of

256   healing, with the medial face shows swelling, and is invaginated into the cavity. Medially, there is

257   a slight overlap of the fragments that make up the lesion showing that after the break occurred

258   and before or during healing one part slipped over the other prior to being fused into their current

259   positions.

260

261   I. This is a deep and elongate lesion with a rimmed margin on the right postorbital (Fig 6). It lies

262   half way down the anterior edge of descending process. The lesion is 18.5 mm in length and 9

263   mm wide (including the raised edges) and with a maximum depth of 2.5 mm. The surface of the

264   lesion shows mildly reactive bone.

265

266   J. There is a light patch of osteomyelitic bone, diagnosed by texture changes, present on the left

267   quadratojugal, in the middle of the element.

268

269   K. In posterior view, the saggital crest is an unusual shape and apparently the two sides have both

270   been damaged though in different ways (Fig 7). Although partly broken, a natural bone surface is

271   present on much of the dorsal margins. The right side has a semicircular section missing, lined by

272   natural bone, and suggestive of a hole in the flange. This is similar in form to an injury seen in a

273   specimen *Troodon* that may have been a cyst (Currie, 1985) or a tooth puncture wound (Tanke &

274   Rothschild, 2002). On the left side of the crest, the dorsal edge curves very rapidly in a ventral

275   direction and, although now broken, would not have met the rising ventrolateral margin. Again

276   however, the edges are natural, suggesting the shape is mostly genuine and not the result of

277   breakage, though this may be pathological or trauma induced. There is only limited distortion

278   elsewhere in the element, suggesting again the feature is probably genuine.

279

280   L. There is damage to the lateral margins of dentary (Fig 8), mostly on the ventral side and these

281   consist of subcircular puncture wounds (including one on the ventral surface), or pairs of

282   elongated ridges that are indicative of former scores. One point on very ventral surface is barely

283   visible in either lateral view, and is represented by a slight bump associated with a slight score.

284   An additional puncture lies on the lateral side of the right dentary lying ventral to the meeting

285   point between the 6th and 7th alveoli. This mark is 4 mm tall by 5 mm long and 1 mm in depth and

286   there is a small rectangular piece of bone that lies on the anterior edge of the mark that appears to

287   have been lifted up (an avulsion) and settled back into place and subsequently fused back with

288   the bone.

289

290   M. On the right surangular are two damage points from preparation and / or excavation (Fig 9).

291   However, there are also two holes in the bone, and a large patch of ostomyelitis of unknown

292   cause. This latter bone type is stronger anteriorly, and then fades towards the mandibular fenestra.

293   Additional osteomyelitic bone lies above and posterior to the fenestra and there is still more along

294   the dorsal edge of this element, including small 'hump' on the posterior part of the surangular

295   (Fig 10).

296

297   N. The posterior carinae of 5th right maxillary tooth has suffered serious ablation, which is here

298   attributed to occlusion wear with the dentary tooth row (Schubert & Ungar, 2005) (Fig 5). The

299   first and third teeth of the right maxilla both have their tips broken and with subsequent wear

300   leading to smoothing of the affected areas. The 11th tooth of the right dentary has also suffered

301   damage which is interpreted here as being a result of premortem malocclusion.

302

303   A number of other very fine marks and cracks are present in places across the cranium and

304   which may represent possible osteopathic marks and traces, but could be taphonomic artefacts

305   based on the partial separation of material and the dorsoventral collapse of the nasals and other

306   parts. As they are minor and difficult to determine their origins, these are not discussed further. In

307   addition to the cranial damage, one dorsal rib shows evidence of having been fractured, but this

308   was well healed at the time of death.

309

310   *Postmortem:*

311

312   Postmortem damage to the specimen is limited and more difficult to determine than

313   premortem injuries that have undergone healing. Postmortem damage on the material is assessed

314   based on the lack of any indications of healing (swelling, reactive bone etc.) with tooth-marks

315   being identified as being sub-parallel marks damaging the bone cortex. One clear set of bite-

316   marks appears on the medial face of the posterior part of the right dentary. A number of other

317   elements show possible evidence of biting with breaks aligning between elements or with

318   localised impacts on bone.

319

320   i. Four tooth marks on posterior medial part of dentary are considered to be the result of biting

321   (Figures 11, 12). These are well spaced (around 15-20 mm between each) and light – they barely

322   graze the surface of the bone. There is no evidence of healing of these implying they were

323   inflicted either postmortem, or very shortly before death. However, the position of these marks on

324   the medial face of the very posterior part of the dentary suggests they were unlikely to be

325   premortem.

326

327   ii. There is a dislodged bone piece between the two posterior most alveoli preserved in the right

328   dentary, and this piece of bone has apparently been forced down into the space between the

329   alveoli (Fig 11, 12). Given that the original position of the dentary as recovered was inverted, this

330   suggests that a strong, but localised impact, broke and drove this fragment into this position, and

331   is therefore indicative of a bite, indeed probably the same one that delivered the sub-parallel

332   damage described above in section (i). We consider this damage to be unlikely to be the result of

333   trampling given that the element is otherwise intact, and not likely due to fluvial action given the

334   relative positions of the dentary and cranium.

335

336   iii. Breaks across the posterior parts of the right dentary as preserved are considered likely the

337   result of a bite. The edges of the breaks are rough and indicative of break of green bone, and are

338   roughly in line with the series of four scores on the dentary described above (i) and the lack of

339   fluvial damage suggests this is postmortem. Similarly, the very dorsal anterior part of the

340   surangular is damaged and may be linked to the bite at the posterior part of the dentary. Part of

341   the dentary posterior to this point has separated from the dentary and is now lost, however there

342   are photographs of this part prior to this loss showing the original condition of the material

343   (Figure 12).

344

345   iv. Approximately 59 mm of the anterodorsal process of the right splenial was broken off when

346   the element was found (Fig 13). There is damage to the dorsal margin of the broken part and the

347   dorsal margin of the splenial as a whole. Restoring this broken process and then placing the

348   whole element in position on the jaw (using Brochu, 2003, figure 40 as a guide) this break aligns

349   very well with the indented bone piece in the dentary (ii) and the associated bite marks (i). This

350 provides evidence that the right mandible was originally complete and one bite (or more, but very

351 close to each other in position and delivery) damaged both the right dentary, and into and

352 through, the posterior part of the right splenial (Fig 14).

353

354 *Indeterminate:*

355

356 There are a number of pieces of the skull that present evidence of damage or breakage, but

357 where it cannot easily be determined if this was damage from trampling, bites, or general

358 disarticulation / erosion etc. Therefore, although these may represent additional evidence for

359 postmortem damage, we take a conservative approach here and do not directly assign them as

360 such.

361

362 1. There is some form of scrape down the dorsal part of the left maxilla, close to the suture with

363 the left nasal.

364

365 2. The left maxilla shows numerous breaks and damage. The base of the left maxilla (4.5 cm

366 posterior to the anterior edge of the antorbital fenestra) is broken as is the ventroposterior part of

367 the maxilla, and some pieces of this element have separated from the main body (Fig 2). These

368 breaks can be aligned with the damage seen to the base of the left lacrimal, which is missing the

369 anterior process and most of the ventral process, as well as the broken palatal shelf. All three

370 areas (maxilla, lacrimal and palatal shelf) show evidence of breaks of green bone, and not just

371 disarticulation or recent erosion. It is at least possible that this area was collectively damaged

372 and / or removed as a result of a single or multiple bites to the area. This is plausible given the

373 clear bite marks to the left dentary that show that a theropod delivered post-mortem bites to the

374 skull, but the lack of distinct tooth marks on this part of the skull make it hard to confirm. This

375 may simply be the result of damage through trampling, but then it would be odd for an animal to

376 step on a skull and break only one side, or leave the palate largely intact while the maxilla was

377 shattered.

378

379 3. The anterior part of left pterygoid is broken and missing. The break occurs in a line with a

380 position approximately in line with the midpoint of the maxilla-jugal suture (based on

381 comparisons with other tyrannosaur skulls) and may be linked to the above described missing

382 portion of the right maxilla and palate (point 2).

383

384 4. The anterior ramus of right palatine is broken with approximately 20 mm of bone missing

385 (based on comparison to the complete left element). The remainder of the anterior ramus is 67.5

386 mm long and was found loose in the quarry, and was later restored to the main body of the right

387 palatine. The posterior parts of both posterior rami of the right palatine are also broken and lost.

388

389 5. The braincase is relatively complete, but the left exoccipital has been broken away at its base

390 and three loose pieces of this were found in the quarry. Two of these pieces can be fitted to the

391 main body with the respective broken edges lining up well. There are no traces of bite marks or

392 punctures, suggesting this was a natural break or through trampling.

393

394 6. A number of marks on the dentary teeth and isolated crowns may be pre- or postmortem and

395 are not considered further as they may be as a result of combat, postmortem damage or

396 malocclusion (Fig 15). Two disarticulated teeth (one already broken) show possible bite marks

397 that are similar tooth marks on tyrannosaurine teeth held in the Tyrrell collections e.g. TMP

398 1988.050.0145, TMP 1988.050.0146 but it is not possible to determine when these marks

399 occurred.

400

Position of elements in field:

401

402   The orientation and position of a number of elements is important to some of the

403   interpretation of the data, and so is described here. Figure 16 is a redrawn version of the quarry

404   map by DHT (who also helped excavate the material and was one of the main preparators of the

405   specimen), which was originally made by the excavation team and provides reference for this

406   description.

407   The intact mandible was found with its ventral edge uppermost and lying over the intact

408   palate with the cranium being inverted and the ventral side uppermost. The premaxillary teeth of

409   the cranium were interlocked with the 4th dentary tooth (approximately – see Fig 17) and the first

410   three premaxillary teeth were not in situ in the cranium, but instead were found inside the palate.

411   The anterior dentary teeth that are missing from the mandible were in the premaxillary-nasals

412   area of the skull, and the missing posterior dentary teeth were located deep in the skull cavity.

413   Collectively this shows that the original position of the dentary was close to natural articulation

414   with the rest of the skull in order for the teeth to fall out and come to lie within the depths of the

415   skull. This also shows that the head could not have been encased in sediment at this time in order

416   for the teeth to have travelled so far down into the skull. We suggest that the dentary was

417   therefore only later moved up and anteriorly, leading to the near separation of the teeth in the

418   dentary and their posteriorly directed alignment – a pattern not seen in the teeth of the premaxilla

419   and maxilla.

420   The femur was buried when the specimen was discovered and excavated and therefore the

421   damage it has suffered (major breaks and crushing) is considered likely to be through trampling

422   and thus Cretaceous in origin. The ilium however was eroded and the damage to this is recent.

423

424

Discussion:

Premortem injury

Studies suggest cranio-facial biting may have been common in tyrannosaurs and possibly other large theropods (Tanke & Currie, 1998; Peterson et al., 2009; Bell & Currie, 2010). Although large carnivores will engage in fights to the death (intra- and interspecifically), either over territory / food or one actively killing another for food, these are rare, if only because of the typically low numbers of large carnivores in an ecosystem. However, animals also try to avoid injury and another large, adult, healthy carnivore is clearly equipped to potentially inflict serious or lethal injuries and if quite different from typical animalian prey (small, juveniles, that also typically lack adult defences such as well-developed horns – Hone & Rauhut, 2010). Currently, evidence of non-avian theropods consuming others (even if there was apparently a large size difference between the consumer and consumed – *Sinocalliopteryx* – Xing et al. 2012) is uncommon, and while these would be expected to be rare, they are clearly occurring. Carnviorous theropods clearly interacted with other live theropods, in at least some cases likely actively hunted and killed them, and consumed dead ones.

Injuries observed on dinosaurs that are hypothesised to be the result of attempted predation by a theropod (e.g. Murphy et al., 2013, DePalma et al 2013) are typically on the body of the intended prey and especially towards the rear of the animal where one might expect a pursuing predatory to strike. Although feeding traces from theropods have been found on the cranium of a consumed dinosaur (Hone et al., 2011) this was notably a situation considered late-stage carcass consumption with bites being normally expected to occur first in the areas of main muscle mass (e.g. the muscles of the pelvis and hindlimbs, viscera etc. – see Hone & Watabe, 2010).

In contrast, injuries hypothesised to be the result of cranio-facial biting are localised on the cranium, implying the animals faced each other directly and thus potentially in some form of

450   ritualised combat. In the case of the specimen here, despite the lack of much of the postcrania,

451   and the injured dorsal rib, it is clear that numerous injuries were inflicted on the skull at some

452   point (and perhaps on multiple occasions) some considerable time before death (see Straight et

453   al., 2009). Based on the size and scale of the injury these would appear to have been inflicted by

454   another large theropod. Their form – punctures, lesions and scrapes are consistent with large and

455   sub-circular teeth and this pattern and positioning seen here is similar to that on another bitten

456   tyrannosaurine skull (Peterson et al., 2009).

457   The most obviously candidate to have inflicted these marks is another tyrannosaurid since

458   these are the only large theropods in the known in the Formation and the damage to the back of

459   the head includes a puncture wound attributable to a large, sub-circular tooth (K – Fig 7) that is

460   characteristic of the group (Holtz, 2004). Given that such ritualised combat would appear to be

461   more likely between two conspecifics than heterospecifics, we conclude that this was likely

462   through engagement with another *Daspletosaurus*. At least one other non-adult tyrannosaurine

463   from the Late Cretaceous of North America shows evidence of cranio-facial biting (Peterson et

464   al., 2009) suggesting such engagements were not limited to mature animals.

465   It is possible that some of the premortem damage to the cranium was inflicted by the pes of a

466   *Daspletosaurus*. Rothschild (2013) recently noted that some injuries to a *Tyrannosaurus* skull

467   may have been inflicted by the feet of a conspecific, and if this is the case, it is reasonable to

468   assume other large-bodied tyrannosaurids may have fought in a similar way. In the case of the

469   damage to the occipital region at least (K) this would appear to be a bite, and we suggest that that

470   in combat between two tyrannosaurines injuries to the head are generally more likely to be

471   inflicted by a mouth than a pes.

472

473   *Postmortem bites*

474   The postmortem bites inflicted on the skull also indicate the bite-maker was a large

475 tyrannosaurid as other carnivorous forms from the Dinosaur Park Formation can be ruled out.

476 The spacing between the marks of the teeth imply a large animal and the possibility that a large

477 part of the skull was bitten through also rules out smaller theropods and small carnivores such as

478 champsosaurs. Azhdarchid pterosaurs may have scavenged on dead animals, but these animals

479 are edentulous and would not have left tooth marks. A number of crocodilians are known from

480 the formation, but these are small (skull length under 50 cm - Wu, 2005) and thus unlikely to

481 have left such large marks and as modern forms at least feed primarily through torsion, these

482 would not be expected to leave such straight bite marks on the tyrannosaur mandible.

483   This immediately suggests that the marks were made by a tyrannosaurid and they do at least

484 bear some resemblance to feeding traces by tyrannosaurines (e.g. Erickson et al., 1996; Hone &

485 Watabe, 2010). Examination of tooth spacing for bite marks is most inexact – although a large

486 space between tooth marks is typically indicative of a large animal, missing or damaged teeth in a

487 jaw can lead to large spaces between teeth, combined with the range of sizes of teeth in the jaw of

488 a single theropod, the difference in spacing between maxillary and premaxillary teeth, the

489 differences in sizes between individuals and intraspecific variation, it may be impossible to tell

490 one species from another from bite marks alone. However, it may be possible to at least rule out

491 some candidates and / determine it bites were made using maxillary teeth or a premaxillary

492 arcade, especially when there is heterodonty as with the tyrannosauids.

493   Using foam we took impressions of the premaxillary and anterior maxillary teeth and the

494 anterior dentary teeth of a number of Dinosaur Park Formation theropods to examine the

495 arrangement of their teeth to compare to the traces seen on the elements here. Given the variation

496 seen within taxa (and especially given the different sizes of even single species) it is difficult to

497 make any firm assessments. However, both the size of, and the spacing between, the marks would

498 appear to rule out small bodied theropods. It is certainly plausible that the mark-maker was a

499 second *Daspletosaurus* and there is nothing to suggest that is was not. As above, given the

500   limited number of tyrannosaurs in the Dinosaur Park Formation, *Daspletosaurus* remains a strong

501   candidate but there is too little information to separate out this from contemporaneous forms.

502   Cannibalism is recorded in *Tyrannosaurus* (Longrich et al., 2010), and it is likely that other

503   theropods, including other tyrannosaurids, fed on each other.

504   The one definitive bite on the *Daspletosaurus* dentary is likely a result of a bite involving the

505   maxillary or non-anteriormost dentary teeth. The premaxillary arcade and / or anterior dentary

506   teeth would be much more closely appressed to one another, even in the largest of

507   tyrannosaurines and so would result in tooth marks that were much closer together, hence the

508   suggestion that these are from a more lateral part of the tooth row. Strong bites from tyrannosaurs

509   seem to be typically delivered with the anterior part of the tooth arcade (Erickson et al., 1996) but

510   these are also used for scrape-feeding to remove flesh from bones (see Hone & Watabe, 2010)

511   which contrasts with the pattern seen here. This may be accidental tooth-on-bone contact

512   therefore, or the result of a bite directs at another part of the skull that left these incidental marks

513   here. Given the apparent delicacy and selective feeding strategies employed by at least one

514   tyrannosaurine, this mark may potentially represent a deliberate feeding strategy, scraping the

515   maxillary teeth alongside the dentary in an attempt to remove muscle tissue, but additional

516   specimens are needed to confirm this hypothesis.

517

518   *Taphonomy / burial and evidence for scavenging.*

519

520   Collectively the specimen most closely resembles Taphonomic Mode B of Eberth and Currie

521   (2005) for the Dinosaur Park Formation. That is, although the specimen is largely incomplete the

522   vast majority of the recovered material relates to a single individual skeleton. These are primarily

523   recovered in palaeochannel facies (Eberth & Currie, 2005) and some common themes in such

524   theropod specimens (their table 24.2) suggest the possibility of local reworking, and that the

525   animal may have died through drowning or disease / injury. Easily transported microvertebrate

526   fossils were found scattered in the matrix that surrounded the tyrannosaur suggesting fluvial

527   action. The preserved microvertebrate specimens (e.g. crocodilian teeth, trionychid turtle plate,

528   crocodilian scute, *Myledaphus* tooth, cf. *Champsosaurus* tooth, salamander vertebra) do not

529   reveal anything unusual with respect to the usual Dinosaur Provincial Park fauna but the presence

530   of champsosaur, crocodylian, and trionychid material among others does also indicate fluvial

531   action. However, the presence and preservation of the small bone bits that could be identified and

532   restored to various parts of the main skull and dentary especially show that the water movement

533   was slow.

534   The specimen as recovered was somewhat dissociated and it is difficult to separate out what

535   of the disarticulation and damage to the skeletal elements may be the result of feeding, and what

536   from simply collapse of a decomposing carcass or possible transport. Certainly the specimen

537   suffered some damage from another theropod, and the damage to the femur suggests damage

538   through trampling. However the lack of much of the postcranium and the presence of elements

539   from other species in the quarry points to a degree of transport in the local area that moved

540   elements around at times.

541   For example, the position of the left jugal and lack of damage compared to the left lacrimal

542   may be as a result of the dissociation of the former, followed by a bite or trampling damaging to

543   the latter, but could also have resulted from a bite damaging the lacrimal with the jugal being

544   separated as a result and falling away (Fig 2). Thus both the positions of marks and breaks on the

545   individual elements (and lost parts or broken rami found elsewhere in the quarry) must be

546   assessed against their likely original positions. Furthermore, a heavy bite on thin bones (as with a

547   cranium) would not leave deep tooth impressions (c.f. Erickson et al., 1996; Hone & Watabe,

548   2010) but instead might lead to shattering, or at least breaking, of elements. Thus tooth marks

549   might not be left or easy to discern, despite a strong bite. Our below inferences are therefore

550   tentative given that some major breaks appear in patterns that imply breakage of multiple aligned

551   elements, but without the definitive evidence that a tooth mark would provide.

552   There is a lack of bite marks on the remaining parts of post-cranial skeleton, including areas

553   where meat would be plentiful on a fresh carcass, or even mid-stage carcass consumption

554   (following Blumenschine, 1979) e.g. the ilium, femur, ribs etc. However, tyrannosaurids seem to

555   leave far more bites on material that do other carnivorous theropods, and even may leave multiple

556   traces with relatively 'careful' feeding (Hone & Watabe, 2010). However, given the amount of

557   missing material it is likely that the specimen was exposed for some time prior to burial. The lack

558   of bite marks may therefore be the result of the loss of much material which could have borne

559   them, although and the lack of shed teeth (both of tyrannosaurs and other small carnivores e.g.

560   see Hone et al., 2011) also collectively suggest that the material was not fed upon extensively.

561   If the animal was relatively well fleshed the when the carnivore fed upon it, then this could

562   have consumed large amounts of material without breaking bones / leaving tooth marks.

563   However, the lack of damage and separation of gastralia and other fine elements like the

564   supradentary suggests this was not part of a normal carcass consumption pattern. The cranium

565   had clearly disintegrated at least in part and elements had separated along suture lines, and not

566   primarily as a result of being bitten.

567   The cranium at least must have been undergoing some decay when the bite occurred. This is

568   based on the extrusion of the dentary teeth, which must have been held in by their ligaments in

569   order not to have fallen out entirely (Fig 8), but still loosely enough attached that they were all

570   partly exuded from their sockets, and also the loose teeth that had fallen into the palate. We

571   cannot easily estimate how long it may have taken for tyrannosaur tooth ligaments to decay and

572   separate, but presumably this would have been days rather than hours and therefore the action

573   that lifted the dentary and repositioned it, presumably coincident with the marks delivered to the

574   dentary, occurred some time after death.

575   Based on the orientation of the dentary teeth and the preserved position of the dentary, this

576   must have been moved anteriorly (Fig 17). Given that it was originally in a natural articulation

577   (based on the dentary teeth lying in the palate), it must have been lifted to come into its final

578   resting place, and could not just be moved forwards easily by fluvial action as the teeth of the

579   dentary and maxilla would have interlocked. The delivery of this bite is also very unlikely to have

580   been during intraspecific combat or a predation event given the position of the bite marks up

581   inside the jaws and how far back they were – the animal would need to have opened the mouth to

582   an extraordinary degree to allow the jaws of the other animal to have reached this position. A

583   decaying carcass however would likely present no such difficulties.

584   As described above, two other areas of damage are hard to confirm as bites as opposed to

585   damage through trampling, but in addition to the damage to, and movement of, the left dentary,

586   there is a possible bite into the right jaw, damaging the right dentary, right splenial and perhaps

587   the right pterygoid and a possible second bite into the left side of the face damaging left lacrimal

588   and left maxilla. The left jugal was displaced and was recovered close to the main part of the

589   skull (see Fig16). If this piece has dissociated through decomposition prior to the putative bite

590   this would explain why this is undamaged, despite the major trauma to that side of the face.

591   There may also have been a bite to the right dentary. Based on *Daspletosaurus* being four

592   teeth in each premaxilla, 17 for each maxilla (Currie, 2003, though he notes this specimen has an

593   unusually low maxillary count and it may be as little as 13) and 18 for each dentary, the total

594   number of teeth in the skull would have been up to 74. A total of 31 teeth are present in situ in the

595   skull and dentary (not including the incipient replacement teeth), and 19 loose teeth were

596   collected from the quarry, for a total of 50 teeth. These teeth match those in the cranium for size,

597   shape and colour and are not considered shed teeth by another animal. Therefore we conclude

598   that originally the other dentary must have been present in the immediate area and shed nearly all

599   of its teeth at some point before it was lost.

600 Finally, the skull is the tallest element of the specimen, and even allowing for stratification of

601 some pieces of the postcranium, may have been the highest up in the quarry. Thus, assuming

602 there was a low level of sediment / water in the environment, the skull may have been the only

603 exposed piece, or the most exposed piece, when the scavenging took place. This is somewhat

604 speculative, but fits the overall pattern of marks on the skull not seen on any other material and

605 the apparent trampling of a buried femur etc. and may therefore explain why one, or even both,

606 dentaries were bitten – they were simply the only exposed part of the skeleton when the

607 encounter took place and thus did not follow the expected carcass consumption patterns.

608 As with the premortem injuries, it is not possible to easily distinguish between cannibalism

609 and feeding by another tyrannosaurid. Currie (2005) notes that *Gorgosaurus* is generally more

610 common in the Dinosaur Park Formation, and thus based simply on numbers would appear to be

611 a more likely candidate to have fed on this animal than a second *Daspletosaurus*. Cannibalism is

612 known in North American tyrannosaurines (Longrich et al., 2010) and thus should not be ruled

613 out in *Daspletosaurus* and certainly it seems most likely that a tyrannosaurid, if not necessarily a

614 conspecific, was responsible for the postmortem feeding traces left here.

615

616 **Conclusions:**

617 In summary, this *Daspletosaurus* skull suffered at least one major postmortem bite, and

618 perhaps three (a second bite to the dentary, and finally one to the left maxilla and associated

619 areas) from another tyrannosaurid, possibly another *Daspletosaurus*. The specimen must have

620 been decaying prior to the delivery of the bite to the dentary, and the condition of other material

621 suggests scavenging, rather than simply late-stage carcass consumption. These interpretations

622 must remain tentative, but this is considered a possible scenario of cannibalistic scavenging and is

623 strong evidence for one large theropod consuming another.

624

References:

Bell PR, Currie PJ. 2010. A tyrannosaur jaw bitten by a confamilial: scavenging or fatal agonism? *Lethaia* 43:278-281

Blumenschine RJ. 1987. Characteristics of an early hominid scavenging niche. *Current Antholopology* 28:383-417.

Brochu CA, 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology Memoir* 7:1–138.

Brusatte SL, Norell MA, Carr TD, Erickson GM, Hutchinson JR, Balanoff AM, Bever GS, Choiniere JN, Makovicky PJ, Xu X. 2010. Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science* 329:1481–1485.

Carpenter K. 2000. Evidence for predatory behavior by carnivorous dinosaurs. *Gaia* 15:135-144.

Carr TD, Williamson TE. 2000. A review of Tyrannosauridae (Dinosauria, Coelurosauria) from New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 17:113-145.

Carr TD, Williamson TE. 2004. Diversity of Late Maastrichtian Tyrannosauridae (Dinosauria:

650   Theropoda) from western North America. *Zoological Journal of the Linnean Society*

651   142:479-523.

652   Charig AJ, Milner AC. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of

653   Surrey. *Bulletin of the Natural History Museum, Geological Series* 53:11-70.

654   Chin K. 1997. What did dinosaurs eat? Coprolites and other direct evidence of dinosaur diets. In:

655   Farlow JO, Brett-Surman MK eds. *The Complete Dinosaur*. Bloomington: Indiana

656   University Press, 371–382.

657   Currie PJ. 1985. Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its

658   bearing on the origin of birds. *Canadian Journal of Earth Sciences* 22:1643-1658.

659   Currie PJ, 2003. Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper

660   Cretaceous of North America and Asia. *Canadian Journal of Earth Sciences* 40:651–665.

661   Currie PJ. 2005. Theropods, including birds. In: Currie, PJ, Koppelhus EB eds. *Dinosaur*

662   *Provincal Park*. Bloomington: Indiana University Press, 367-397.

663   DePalma RA, Bumham DA, Martin LD, Rothcschild BM, Larson PL. 2013. Physical evidence of

664   predatory behaviour in *Tyrannosaurus rex*. *Proceedings of the National Academy of*

665   *Sciences* 110:12560-12564.

666   Eberth DA, Currie PJ. 2005. Vertebrate taphonomy and taphonomic modes. In: Currie, PJ,

667   Koppelhus EB eds. *Dinosaur Provincal Park*. Bloomington: Indiana University Press, 453-

668   477.

669   Erickson GM, Olson KH. 1996. Bite marks attributable to *Tyrannosaurus rex*: Preliminary

670   description and implications. *Journal of Vertebrate Paleontology* 16: 175-178.

671   Erickson GM, van Kirk SD, Su J, Levenston ME, Caler WE, Carter DR. 1996. Bite-force

672   estimation for *Tyrannosaurus rex* from bone-marks. *Nature* 382: 706-708.

673   Fowler DW, Freedman EA, Scannella JB, Kambic RE. 2011. The Predatory Ecology of

674   *Deinonychus* and the Origin of Flapping in Birds. *PLoS ONE* 6:e28964.

675   Holtz TR. 2004. Tyrannosauroidea. In: Weishampel DB, Dodson P, Osmólska H eds. *The*

676   *Dinosauria (second edition).* Berkeley: University of California Press, 111–136.

677   Holtz TR. 2008. A critical reappraisal of the obligate scavenging hypothesis for *Tyrannosaurus*

678   *rex* and other tyrant dinosaurs. In: Larson P, Carpenter K eds. Tyrannosaurus rex *the Tyrant*

679   *King*. Bloomington: Indiana University Press, 371-396.

680   Hone DWE, Rauhut OWM. 2010. Feeding behaviour and bone utilisation by theropod dinosaurs.

681   *Lethia* 43:232-244 .

682   Hone DWE, Watabe M, 2010. New information on the feeding behaviour of tyrannosaurs. *Acta*

683   *Palaeontologica Polonica* 55:627–634.

684   Hone DWE, Choiniere J, Sullivan C, Xu X, Pittman M, Tan Q. 2010. New evidence for a tropic

685   relationship between the dinosaurs *Velociraptor* and *Protoceratops*. *Palaeogeography,*

686   *Palaeoclimatology, Palaeoecology* 291:488-492.

687   Hone DWE, Wang K, Sullivan C, Zhao X, Chen S, Li D, Ji S, Ji Q, Xu X. 2011. A new, large

688   tyrannosaurine theropod from the Upper Cretaceous of China. *Cretaceous Research,*

689   32:495-503.

690   Hone DWE, Tsuhiji T, Watabe M, Tsogbataar K. 2012. Pterosaurs as a food source for small

691   dromaeosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 331:27-30.

692   Hurum JH, Sabath K. 2003. Giant theropod dinosaurs from Asia and North America: skulls of

693   *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. *Acta Palaeontologica Polonica*

694   48:161–190.

695   Jacobsen AR. 1998. Feeding behavior of carnivorous dinosaurs as determined by tooth marks on

696   dinosaur bones. *Historical Biology* 13:17–26.

697   Larsson HCE, Hone DWE, Dececchi TA, Sullivan C, Xu X. 2010. The winged non-avian

698   dinosaur *Microraptor* fed on mammals: implications for the Jehol Biota ecosystems.

699   *Journal of Vertebrate Paleontology* 30:39A.

700 Longrich NR, Horner JR, Erickson GM, Currie PJ (2010). Cannibalism in *Tyrannosaurus rex*.

701   *PLoS ONE* 5: e13419.

702 Murphy NL, Carpenter K, Trexler D. 2013 New evidence for predation by a large tyrannosauird.

703   In: Parrish JM, Molnar RE, Currie PJ, Koppelhus EB eds. *Tyrannosaurid paleobiology*.

704   Bloomington: Indiana University Press, 279-286.

705 O'Connor J, Zhou Z, Xu X. 2011. Additional specimen of *Microraptor* provides unique evidence

706   of dinosaurs preying on birds. *Proceedings of the National Academy of Sciences*,

707   108:19662–19665.

708 Ostrom JH. 1978. The osteology of *Compsognathus longipes* Wagner. *Zitteliana* 4:73-118.

709 Peterson JE, Henderson MD, Scherer RP, Vittore CP. 2009. Face biting on a juvenile

710   tyrannosaurid and behavioural implications. *Palaios* 24:780-784.

711 Rayfield EJ. 2004. Cranial mechanics and feeding in *Tyrannosaurus rex*. *Proceedings of the*

712   *Royal Society of London, Series B* 271:1451–59.

713 Rayfield EJ. 2005. Aspects of comparative cranial mechanics in the theropod dinosaurs

714   *Coelophysis, Allosaurus* and *Tyrannosaurus*. *Zoological Journal of the Linnean Society*

715   144:309–16.

716 Rothschild BM. 2013. Clawing their way to the top: tyrannosaurid pathology and lifestyle. In:

717   Parrish JM, Molnar RE, Currie PJ, Koppelhus EB eds. *Tyrannosaurid paleobiology*.

718   Bloomington: Indiana University Press, 211-221.

719 Rothschild BM, Martin LD. 1993. *Paleopathology – Disease in the Fossil Record.* CRC Press:

720   Boca Raton.

721 Russell DA. 1970. *Tyrannosaurs from the Late Cretaceous of western Canada*. Queen's Printer.

722 Schubert BW, Ungar PS. 2005. Wear facets and enamel spalling in tyrannosaurid dinosaurs. *Acta*

723   *Palaeontologica Polonica* 50:93-99.

724 Straight WH, Davis GL, Skinner CW, Haims A, McClennan BL, Tanke DH. 2009. Bone lesions

725   in hadrosaurs: Computed Tomographic Imaging as a guide for paleohistologic and stable-

726   isotopic analysis. *Journal of Vertebrate Paleontology* 29:315-325.

727 Tanke D, Currie P. 1998. Head-biting behavior in theropod dinosaurs: Paleopathological

728   evidence. *Gaia* 15: 167–184.

729 Tanke DH, Rothschild BM. 2002. An annotated bibliography of dinosaur paleopathology and

730   related topics. *New Mexico Museum of natural history and Science Bulletin* 20:1839-1999.

731 Varricchio DJ. 2001. Gut contents from a Cretaceous tyrannosaurid: implications for theropod

732   dinosaur digestive tracts. *Journal of Paleontology* 75:401–406.

733 Wu X. 2005. Crocodylians. In: Currie PJ, Koppelhus EB eds. *Dinosaur Provincal Park*.

734   Bloomington: Indiana University Press, 277-291.

735 Xing L, Bell PR, Persons WS IV, Ji S, Miyashita T, Ji Q, Currie. 2012, PJ. Abdominal contents

736   from two large compsognathids demonstrate feeding on dromaeosaurids and

737   confuciusornithids. *PLoS ONE 7:*e44012.
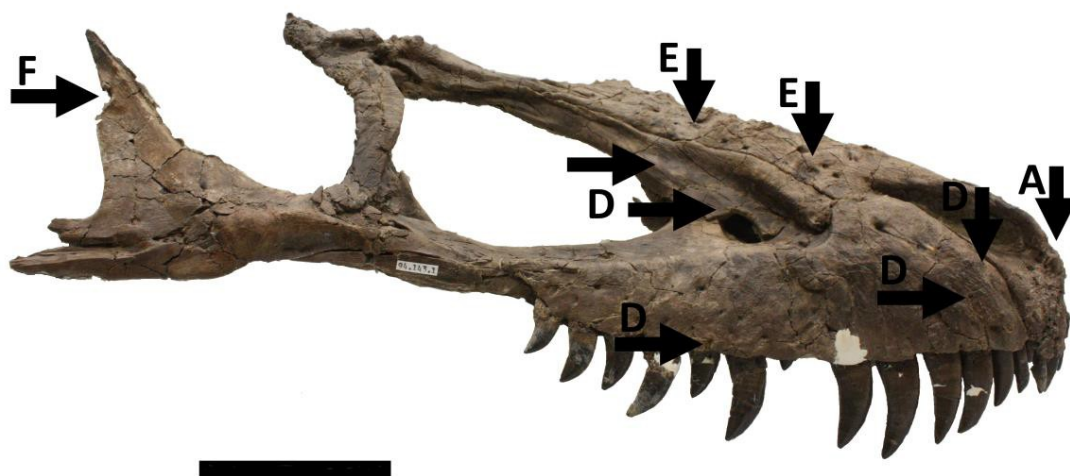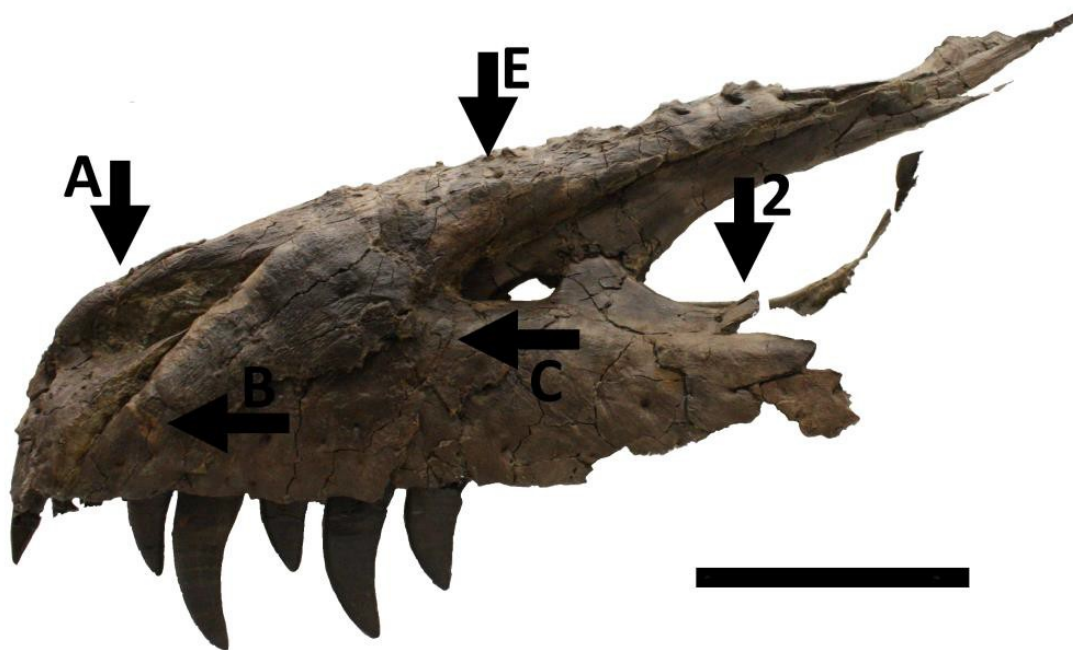
738

739

740 **Figures:**

741

742 Fig 1. Skull in right lateral view showing numerous injuries indicated with black arrows and the

743   relevant code letter (see the text for details). See also figures 4 and 5 for additional details

744   on the right maxilla not indicated on this figure for clarity. Scale bar is 100 mm.

745

746   Fig 2. Skull in left lateral view showing numerous injuries indicated with black arrows and the

747   relevant code letter or number (see the text for details). Note that for this view the 'floating

748   effect' of a thin lacrimal and other posterior elements is due to the fact that these are

749   supported by plaster which has been digitally edited out so not all of the medial side of the
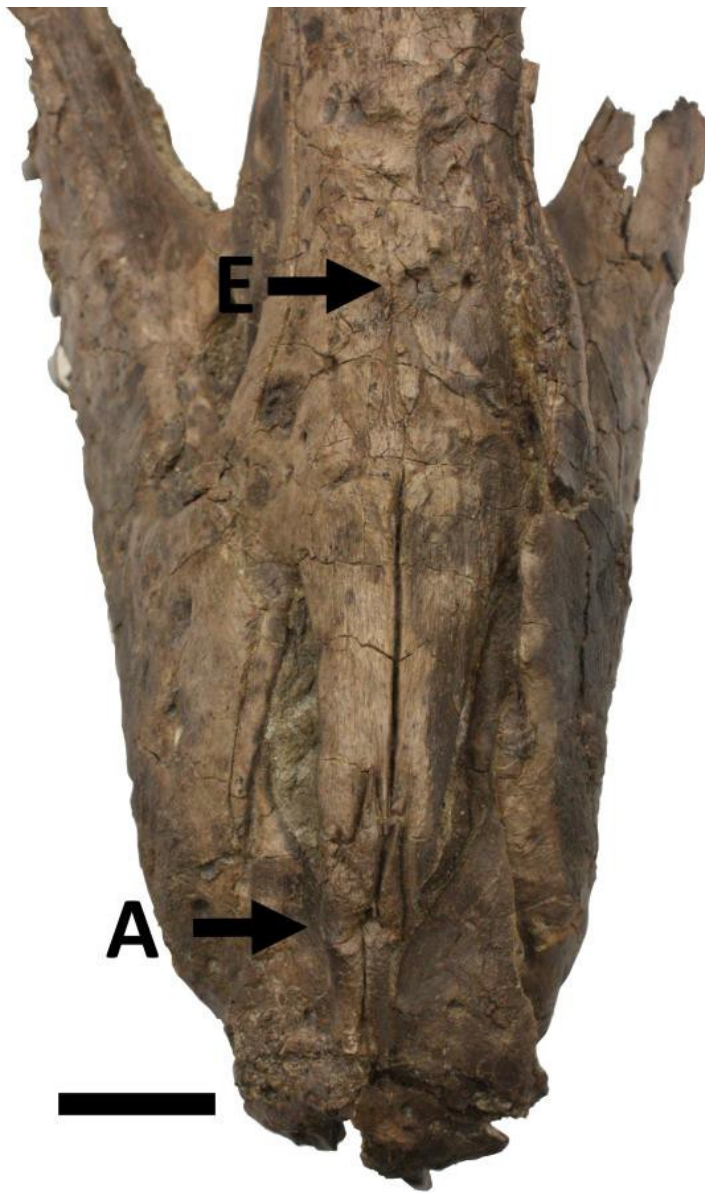
750   bone can be seen. Scale bar is 100 mm.

751

752   Fig 3. Snout in dorsal view showing damage A to the ascending processes of the premaxillae and

753   E, a large subcircular lesion in the nasals. Scale bar is 50 mm.

754

755

756 Fig 4. Lesion above the accessory maxillary fenestra described in D (black arrow). Scale bar is 10
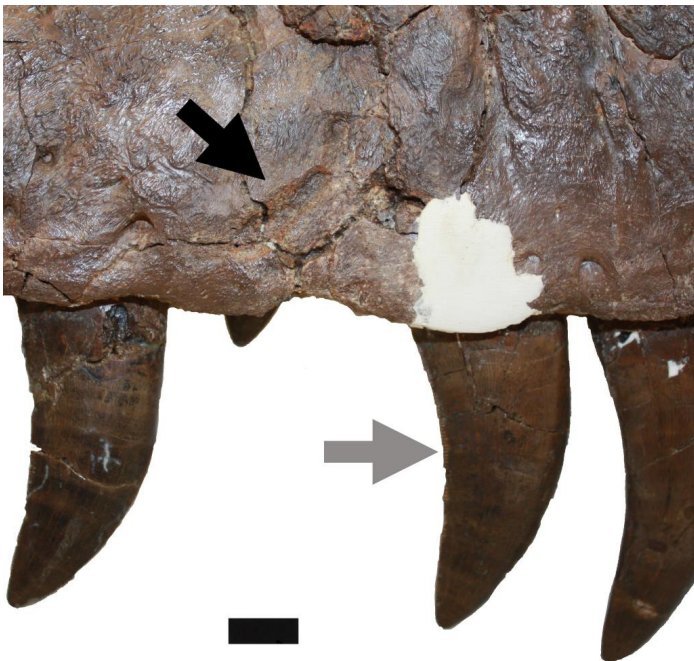
757   mm.

758

759

760 Fig 5. Damage to the right maxilla described in D (upper black arrow). Also indicated is the

761   damage to the posterior carina of the maxillary tooth described in N (grey arrow). Scale
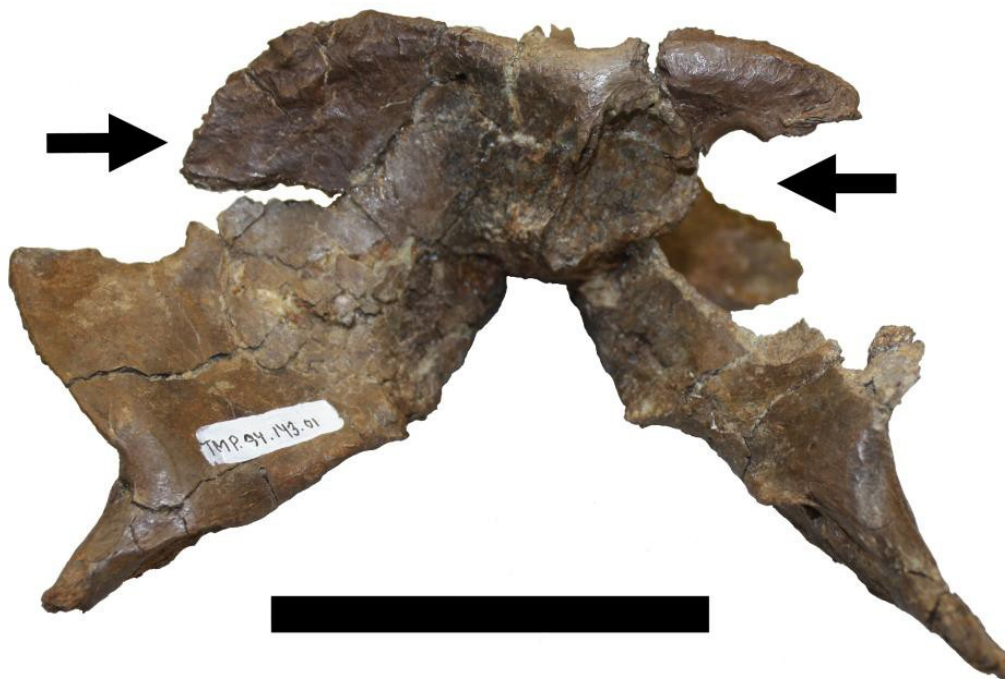
762   bare is 10 mm.

763

764   Fig 6. Damage H and I to the left postorbital. Scale bar is 50 mm.

765

766

767   Fig 7. Damage K to the two sides of the occipital region (in posterior view). On the left side the

768   dorsolateral part has been removed, and on the right, a large subcircular puncture has

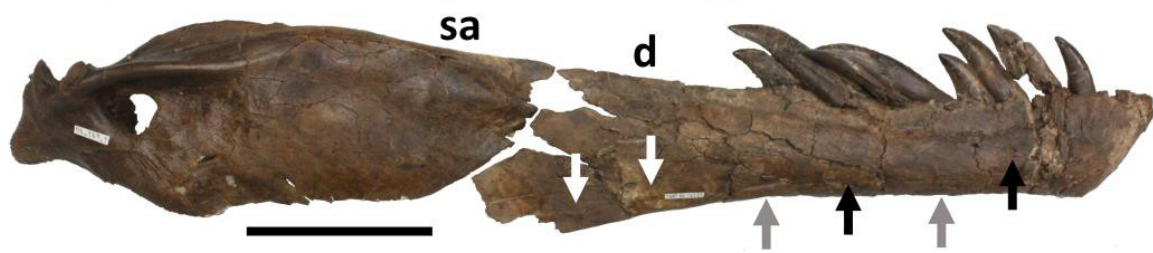769   penetrated the bone. Scale bar is 50 mm.

770

771   Fig 8. Approximate reconstruction of the lateral elements of the right mandible with damage L to

772   the lateral face and to the ventral margin of the dentary indicated. Punctures are indicated

773   with black arrows, ridges on the lateral face of the bone are in white arrows and grey

774   arrows indicate the location of marks on the underside of the bone. Abbreviations: d,

775   dentary; sa surangular. Scale bar is 100 mm.
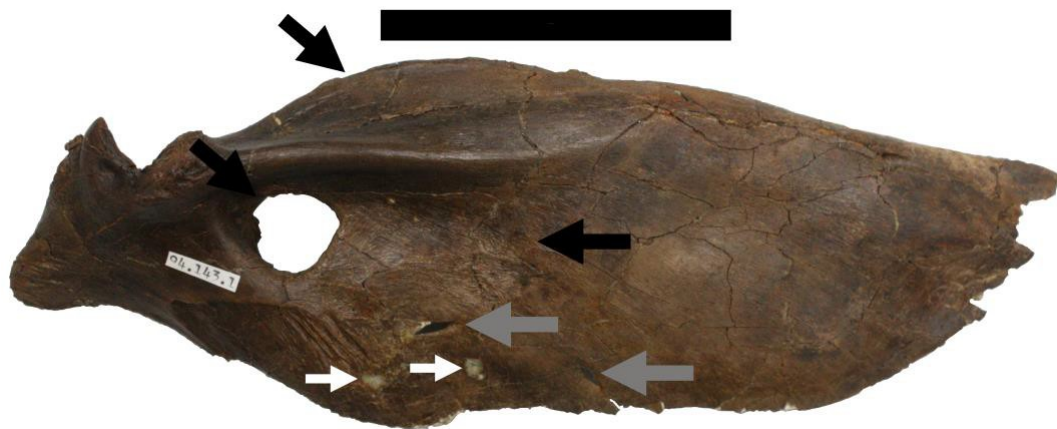
776

777

778   Fig 9. Damage M to the right surangular. Several areas showing osteomyelitic bone are indicated

779   with black arrows. Two holes that appear to be a result of damage are indicated with grey

780   arrows, and two holes that are preparation marks are indicated with smaller white arrows.

781   Scale bar is 100 mm.

782

783

784

785   Fig 10. Close up of the major patch of osteomyeltic bone on the right surangular (central part of

786   the image). Scale bar is 20 mm.

787

788   Fig   11.

789   Damage i, ii and iii to the posterior medial part of the right dentary. A series of vertically

790   aligned scores (i) and a break in the bone (ii), and damage to the lower part of the dentary

791   (iii) likely as a result of postmortem bites. This shows the element as currently preserved

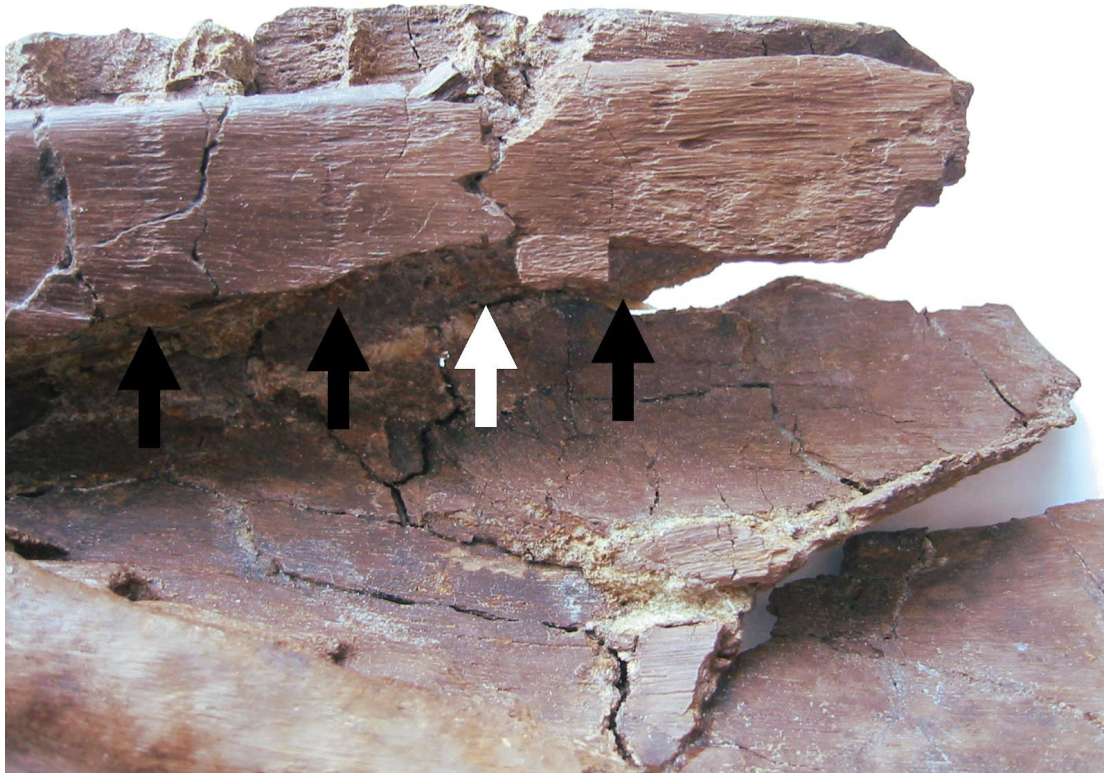792   where a fragment of bone is missing posterior to ii - see also figure X. Scale bar is 20 mm.

793

794   Fig   12.

795   Damage i and ii as seen prior to the loss of the part of the dentary to the right of the break

796   from damage ii (white arrow). The bite marks on the medial surface of i (black arrows) are

797   also clearly seen.

798

799

800   Fig 13. Right splenial in medial view showing damage iv. The part to the right of the black arrow

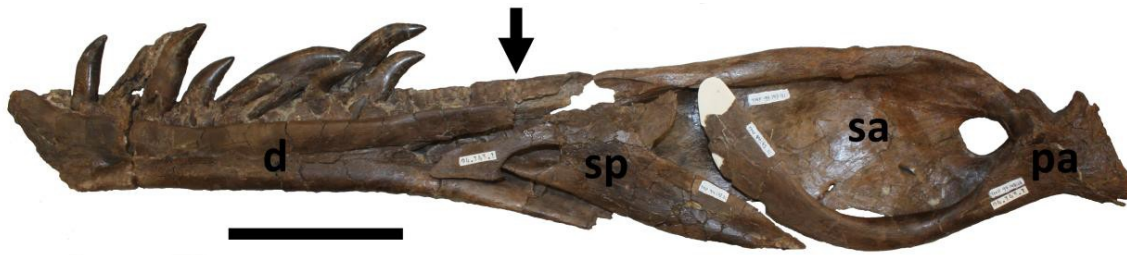801   indicates the piece that was separated. Scale bar is 100 mm.

802

803   Fig 14.

804   Approximate reconstruction of the elements of the right mandible in medial view. Note that

805   the black arrow indicates the damage ii inflicted on the dentary (see Figure 11) is closely

806   aligned to the break on the anterior part of the splenial (Figure 13), suggesting the two

807   breaks may have occurred as the result of a single bite. Abbreviations: d, dentary; sp,

808   splenial; sa surangular; pa, prearticular. Scale bar is 100 mm.

809

810

811   Fig 15. Isolated dentary tooth showing occlusal wear on the enamel (damage 6). Scale bar is 10

812   mm.

813

?CP

PCV

VFR

DRF

DR

GF

CH

DRF

DR

DR

DNS

CV

Q

DR

CVV

CH

DV

DR

CR

CR

CR

GF

DV

CR

CVV

DR

Quarry margin

DR

CR

SK

DR

LS

CV

CV

SQ

J

BC

PT

CV

PA

CV

CV

QJ

LC

IL

Q

PO

DV

CV

CH

FE

IL

VF

CV
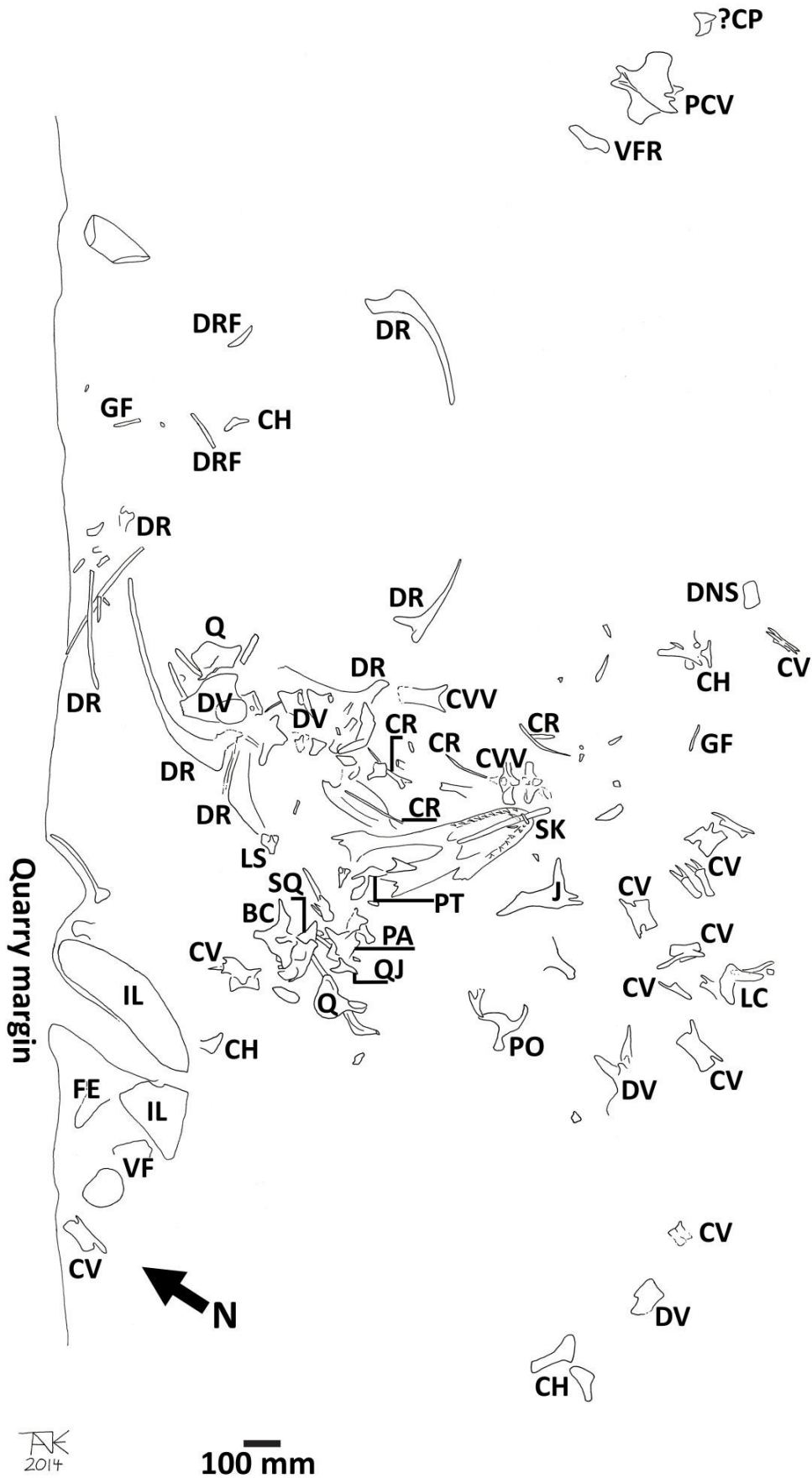
DV

CV

CH

AK
2014

100 mm

N

815   Fig 16. Quarry map of the *Daspletosaurus*. Key to elements is as follows: BC, braincase; CH,

816   chevron; ?CP, coronoid process; CR, cervical rib; CV, caudal vertebra; CVV, cervical

817   vertebra; DNS, dorsal neural spine; GF, gastralium fragment; DR, dorsal rib; DRF, dorsal

818   rib fragment; DV, dorsal vertebra; FE, partial femur; Il, ilium; J, jugal; LC, lacrimal; LS,

819   laterosphenoid; PA, prearticular; PCV, proximal caudal vertebra; PO, postorbital; PT,

820   pterygoid; Q, quadrate; QJ, quadratojugal; SK, skull (major piece including a dentary); VF,

821   vertebral fragment. Fragmentary elements that can be identified as belonging to the

822   skeleton are illustrated but not labeled, and elements from other taxa are not shown. North

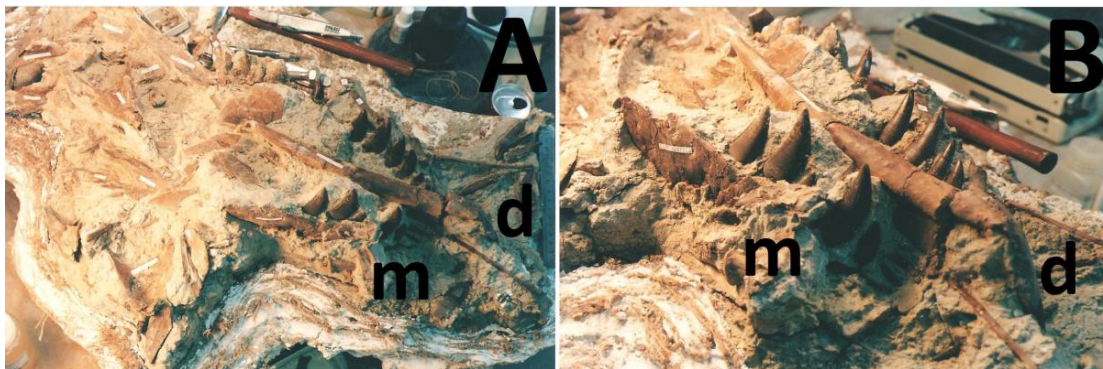823   is indicated on the map, and the scale bar is 100 mm.

824

825   Fig   17.

826   The specimen under preparation showing the position of the right dentary relative the main

827   part of the skull (see also Fig 16). A: in laterodorsal view with the maxilla (m) and dentary

828   (d) visible, and B: in anteriodorsal view. The dentary is offset from its natural position but

829   also moved considerably anteriorly.

830