Evidence for the Cretaceous shark *Cretoxyrhina mantelli* feeding on the pterosaur *Pteranodon* from the Niobrara Formation

David W E Hone Corresp., 1 , **Mark P Witton** 2 , **Michael B Habib** 3

1 School of Biological and Chemical Sciences, Queen Mary University of London, London, United Kingdom

2 School of Earth and Environmental Sciences, University of Portsmouth, Portsmouth, United Kingdom

3 Keck School of Medicine, University of Southern California, Los Angeles, United States

Corresponding Author: David W E Hone
Email address: d.hone@qmul.ac.uk

A cervical vertebra of the large, pelagic pterodactyloid pterosaur *Pteranodon* sp. from the Late Cretaceous Niobrara Formation of Kansas, U.S.A is significant for its association with a tooth from the large lamniform shark, *Cretoxyrhina mantelli*. Though the tooth does not pierce the vertebral periosteum, the intimate association of the fossils – in which the tooth is wedged below the left prezygapophysis – suggests their preservation together was not mere chance, and the specimen is evidence of *Cretoxyrhina* biting *Pteranodon*. It is not possible to infer whether the bite reflects predatory or scavenging behaviour from the preserved material. There are several records of *Pteranodon* having been consumed by other fish, including other sharks (specifically, the anacoracid *Squalicorax kaupi*), and multiple records of *Cretoxyrhina* biting other vertebrates of the Western Interior Seaway, but until now interactions between *Cretoxyrhina* and *Pteranodon* have remained elusive. The specimen increases the known interactions between large, pelagic, vertebrate carnivores of the Western Interior Seaway of North America during the Late Cretaceous, in addition to bolstering the relatively small fossil record representing pterosaurian interactions with other species.

1   **Evidence for the Cretaceous shark *Cretoxyrhina mantelli* feeding on the pterosaur *Pteranodon***

2   **from the Niobrara Formation**

3   **David W. E. Hone[1]***

4   **Mark P. Witton [2]**

5   **Michael B. Habib[3]**

6   1. School of Biological and Chemical Sciences, Queen Mary University of London, London, E1

7   4NS, UK.

8   2. School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Road,

9   Portsmouth PO1 3QL, UK.

10   3. Keck School of Medicine, University of Southern California, Los Angeles, CA,

11   United States of America

12   **Corresponding author:** David Hone, d.hone@qmul.ac.uk

15   **Abstract:**

16   A cervical vertebrae of the large, pelagic pterodactyloid pterosaur *Pteranodon* sp. from the Late

17   Cretaceous Niobrara Formation of Kansas, U.S.A is significant for its association with a tooth

18   from the large lamniform shark, *Cretoxyrhina mantelli*. Though the tooth does not pierce the

19   vertebral periosteum, the intimate association of the fossils – in which the tooth is wedged

20   below the left prezygapophysis – suggests their preservation together was not mere chance,

21   and the specimen is evidence of *Cretoxyrhina* biting *Pteranodon*. It is not possible to infer

22   whether the bite reflects predatory or scavenging behaviour from the preserved material.

23   There are several records of *Pteranodon* having been consumed by other fish, including other

24   sharks (specifically, the anacoracid *Squalicorax kaupi*), and multiple records of *Cretoxyrhina*

25   biting other vertebrates of the Western Interior Seaway, but until now interactions between

26   *Cretoxyrhina* and *Pteranodon* have remained elusive. The specimen increases the known

27   interactions between large, pelagic, vertebrate carnivores of the Western Interior Seaway of

28   North America during the Late Cretaceous, in addition to bolstering the relatively small fossil

29   record representing pterosaurian interactions with other species.

30

31   **Introduction:**

32   *Pteranodon* is a large pterodactyloid pterosaur from the Late Cretaceous (Coniacian-

33   Campanian) of North America with an estimated maximum wingspan of 7.25 m (Bennett,

34   2001). The genus was among the first pterosaurs reported from North America (Marsh, 1876 –

35   see Bennett, 2001 and Witton, 2010 for context of its discovery) and has become one of the

36   best known flying reptiles thanks to a representation of over 1100 specimens – the highest

37   sample size for any pterosaur genus. Although most specimens are incomplete and crushed,

38   every component of its osteology is known and has been described in detail (Eaton, 1910;

39   Bennett, 1991, 1994, 2001, 2017, 2018; Bennett & Penkalski, 2018). As a result of the number

40   of available specimens, its long research history and comprehensive documentation, the genus

41   has become a cornerstone of pterosaur research. *Pteranodon* has been an important animal for

42   understanding pterosaur flight (Hankin & Watson, 1914; Bramwell & Whitfield, 1974; Stein,

43   1975), the evolution of giantism in flying animals (Witton & Habib, 2010), pterosaur ontogeny

44   (Bennett, 1993), and palaeoecology (Bennett, 2001; Witton, 2018).

45   The majority of *Pteranodon* specimens are known from the Late Cretaceous Niobrara

46   Formation from Kansas, U.S.A., a marine deposit created by the Western Interior Seaway,

47   though other specimens also occur in additional formations in Wyoming and South Dakota

48   (Bennett, 1994, 2001). Niobrara specimens of *Pteranodon* occur in localities that were

49   hundreds of kilometres from the palaeocoastline and this, along with a number of aspects of

50   functional anatomy, has seen the genus long interpreted as a seagoing, pelagic animal (e.g.,

51   Bennett, 2001; Witton, 2013, p. 179).

52   *Pteranodon* was likely an important component of the Western Interior Seaway

53   ecosystem. It seems to have been relatively abundant, being known from both a large number

54   of fossils and making up some 97% of Niobrara Formation pterosaur finds. It was also a large

55   animal - Bennett (1993) identified a bimodal size distribution among the large *Pteranodon*

56   sample where two thirds of individuals were c. 3.5 m in wingspan, and the remaining third were

57   much larger, some exceeding 6 m across the wings (Bennett, 2001). Larger specimens likely

58   exceed the masses of any flying bird, extant or extinct, with estimated body masses of 35-50 kg

59   for animals of 6 m wingspan (Paul, 2002; Witton, 2008; Henderson 2010), compared to 21.9–

60   40.1 kg in the largest fossil flying birds, the pelagornithids (Mayr & Rubilar-Rogers, 2010;

61   Ksepka, 2014). *Pteranodon* populations may therefore have been major consumers in the

62   Western Interior Seaway ecosystem, as well as potentially sources of food for other animals.

63   However, our understanding of interactions between *Pteranodon* and other Seaway

64   taxa are limited. As with other pterosaur species, few *Pteranodon* fossils preserve remains of

65   ingested content and they only rarely record evidence of consumption by other animals

66   (Witton, 2018). Regurgitated fish are preserved in the gular region of one *Pteranodon* specimen

67   (Brown, 1943; Bennett, 2001, 2018) and some palaeoecological significance has been ascribed

68   to small fish vertebrae found in association with *Pteranodon* fossils (Bennett, 2001; Hargrave,

69   2007; Ehret & Harrell, 2018). Biting traces on *Pteranodon* elements show that some individuals

70   were eaten by the anacoracid shark *Squalicorax kaupi* as well as a saurodontid fish, most likely

71   *Saurodon* or *Saurocephalus* (Witton, 2018; Ehret & Harrell, 2018). The record of pterosaur

72   ecological interactions is sufficiently sparse that any fossilised interactions with other species

73   should be put on record, so we hereby report on a series of *Pteranodon* cervical vertebrae,

74   LACM 50926, associated with a tooth of the lamniform shark *Cretoxyrhina mantelli*. This is first

75   documented occurrence of this large shark interacting with any pterosaur.

76

77   **Systematic nomenclature:**

78   The taxonomy of *Pteranodon* is a matter of recent dispute. For the last two decades

79   most workers have followed the treatment of the genus outlined by Bennett (1994), who made

80   a case for reducing the 11 binomials associated with *Pteranodon* (excluding those names

81   related to *Nyctosaurus*) to two sexually dimorphic chronospecies: the older *Pteranodon*

82   *sternbergi* and the younger *P. longiceps*. In this scheme, the skulls of these species are

83   distinguished by details of their cranial crests, and (more tentatively) occiput orientation and

84   mandibular ramus depth. Postcranial bones of these specimens are nearly identical and of little

85   taxonomic utility (Bennett, 1994). More recently, Kellner (2010) argued for *Pteranodon sensu*

86   Bennett (1994) being comprised of four species in three genera. While agreeing with Bennett

87   (1994) that all 'historic' *Pteranodon* species were problematic excepting *longiceps* and

88   *sternbergi*, Kellner (2010) created a multi-taxic pteranodontid assemblage for the Niobrara

89   specimens comprising *Pteranodon longiceps*, *Geosternbergia* (rather than *Pteranodon*)

90   *sternbergi*, and two novel species, *Geosternbergia maiseyi* and *Dawndraco kanzai*. These taxa

91   are primarily distinguished by headcrest morphology and details of the posterior skull, as well

92   as finer stratigraphic divisions of the Niobrara Formation (Kellner, 2010) than the broader

93   'upper' and 'lower' divisions of the Smoky Hill Chalk *Pteranodon* fauna recognised by other

94   workers (e.g. Bennett, 1994; Everhart, 2005; Carpenter, 2008). Subsequent criticism of this

95   proposal has questioned the validity of the proposed differences between at least *Dawndraco*

96   and *Pteranodon* sensu Bennett, noted incongruence between the stratigraphic divisions

97   signified by Kellner (2010) against other Niobrara Formation taxa, as well as the lack of

98   statistical support for splitting *Pteranodon* into multiple genera, compared to the strong

99   statistical support for Bennett's interpretation (Martin-Silverstone et al., 2017; Acorn et al.,

100   2017). We thus follow several other works (Witton, 2013, 2018; Bennett 2016, 2017, 2018) in

101   retaining Bennett's (1994) treatment of *Pteranodon* here. Note however that discussion of

102   *Pteranodon* taxonomy is ongoing (Brandão & Rodrigues, 2018).

103

104   **Materials and Methods:**

105   LACM 50926 (Los Angeles County Museum of Natural History, USA) is a specimen of

106   *Pteranodon* mounted in a large glass case for public display at the Los Angeles County Museum

107   of Natural History and is difficult to access directly (Fig 1). The specimen has a large

108   *Cretoxyrhina mantelli* tooth intimately associated with the fourth cervical vertebra (Fig 2). Parts

109   of the mount are genuine, well preserved fossils showing only limited crushing compared to

110   many specimens of the genus. However, several elements are reconstructed to replace missing

111   parts and the mount is a composite of material from several individuals (see Bennett, 1991,

112   2001), as is obvious from bone size discrepancies between several neighbouring elements (Fig.

113   1). Bennett (pers. comm. 6/ 2016) also notes material accessioned under this number (much of

114   it in collections space and not in the exhibit mount) includes three mandibular rami, confirming

115   the multi-individual nature of this specimen. An alternate specimen number (65218) occurs on

116   the mandible and the cervical bearing the shark tooth, but this cannot be seen on other

117   elements. This may indicate that the mandible and cervical were associated when discovered.

118   Bennett (2001) was able to identify many of the LACM 50926 forelimb elements as belonging to

119   a single individual, although there are no records to indicate which parts of the mounted

120   specimen might relate directly to the cervical series. The preservation quality and size of the

121   vertebrae correspond well to the other elements (including the forelimb bones) and this implies

122   that LACM 50926 may represent much of a skeleton. However, the absence of both

123 anteriormost and posterior cervical vertebrae means no anatomical continuity links the 50926

124 vertebrae with the rest of the material, and their association to the rest of the skeleton cannot

125 be confidently assumed.

126   Notes held at the LACM show that the specimen was collected in 1965 by M.C. Bonner

127 from Niobrara Chalk 23, Niobrara Formation, Logan County, Kansas. Bennett (1991) refers to

128 two specimens under this number (LACM 50926 and 50926 "A") and concurs with this locality,

129 adding that they were collected between Marker Units 14 and 19. This makes a Santonian age

130 likely for LACM 50926 (Hattin, 1982; Bennett, 1994).

131

132 **Description:**

133   The anatomy of *Pteranodon* has been described in detail elsewhere (Bennett, 2001) and

134 we will therefore focus exclusively on the association between the shark tooth and pterosaur

135 material. The cervical vertebra bearing the shark tooth is preserved in contact with two other

136 cervicals as a series of three elements. Thus, within the composite context of the LACM

137 specimen, these vertebrae at least can be safely considered part of a single individual. The

138 cervicals are preserved with contact between the successive post- and prezygapophyses. These

139 are identified by Bennett (2001) as cervical vertebrae 4-6, and he also identified a preceding,

140 though not articulated, cervical in the LACM 50926 mount as a cervical 3. The vertebrae retain

141 some three-dimensionality, although they are partially crushed at an oblique angle, shearing

142 them along their midline such that the left sides are depressed and right sides elevated (Figs 1-

143 2). The neural spine is missing (now restored) from cervical 4 and parts of the neural spines of

144   cervicals 5 and 6 are damaged. Damage to the bone cortex reveals the internal structure of the

145   bones in all three vertebrae.

146   The centrum lengths of the three cervical vertebrae in the series have been measured as

147   69.0, 77.8, and 71.5 mm respectively (Bennett, 2001). Based on comparisons to other

148   specimens (see Bennett, 2001) this would correspond to a *Pteranodon* with a c. 5 m wingspan,

149   and was presumably therefore osteological adult or near adult in size. The embedded shark

150   tooth is approximately 24 mm in total height (root plus crown) (this was measured from

151   photographs as it was impossible to measure the tooth given its location and the mount of the

152   specimen), subtriangular in shape and highly compressed labiolingually. A wide, lunate root is

153   formed from two obtusely angled, swollen root lobes. The termination of the left lobe (viewed

154   from lingual aspect) forms a broad, somewhat rounded surface, but the termination of the right

155   lobe is missing (Fig. 2). The crown is swollen on the labial surface, c. 12 mm long (measured

156   from the base of the root to apex of the crown), almost symmetrical but not significantly

157   recurved with respect to the root. No serrations are apparent on the tooth crown but the

158   lateral and medial crown edges are somewhat worn with chipped margins. The tooth

159   enameloid is bright white with grey to brown patches, and the root is pale grey-brown and

160   close in colour to that of the pterosaur elements.

161   The tooth lies between the left prezygapophysis of cervical 4 and the centrum. In some

162   aspects it appears that the tooth is wedged or has cut into the base of the prezygapophysis and

163   the centrum however, it lies medial to the prezygapophysis and does not directly contact this

164   projection. The tooth is preserved at a shallow angle to the long axis of the vertebra (though

165   this may reflect the crushing of the specimen rather than its original orientation) and the apex

166   of the crown faces posteriorly and ventrally with respect to the vertebral corpus. Although the

167   tip of the tooth does not appear to penetrate the centrum, the tip of the tooth contacts it.

168

169   **Results:**

170   *Taxonomic identities:*

171   The composite nature of LACM 50926 complicates discussions of its affinities, but there

172   is no doubt that the specimen can be referred to *Pteranodon* given its provenance and

173   matching anatomy to this pterosaur (Eaton, 1910; Bennett, 2001). Identification to species level

174   is more problematic as *Pteranodon* taxonomy is exclusively informed by the posterior skull

175   region (e.g. Eaton, 1910; Bennett, 1994; Kellner, 2010), and the vertebra is not associated with

176   any skull material. Following Bennett's (1994) tentative suggestion that *P. sternbergi* may have

177   a shallower mandible than *P. longiceps* we compared the LACM 50926 mandibular ramus with

178   specimens referred to these species. However, we were unable to determine a significant

179   match with either taxon. Hargrave (2007) suggested that the tomial margins of posterior *P.*

180   *longiceps* mandibles are curved, and this morphology is present in the LACM 50926 mandible.

181   However, while we agree this can be seen in some *P. longiceps* (e.g. YPM 2594 - YPM, Yale

182   Peabody Museum, USA) it does not seem to be a universal trait (e.g. YPM 1177).

183   The recovery of LACM 50926 from marker units 14-19 of Hattin's (1982) Smoky Hill

184   Chalk stratigraphy gives it provenance among younger Niobrara beds yielding *Pteranodon*

185   *longiceps* rather than *P. sternbergi* (Bennett, 1994; Carpenter, 2008, although Kellner, 2010

186   argues that species more closely related to *P. sternbergi* than *P. longiceps* may persist into

187   younger deposits). This indicates that LACM 50926 probably represents *P. longiceps* but, in lieu

188   of diagnostic fossil material, we regard the specimen as *Pteranodon* sp.

189   A number of medium- to large-sized, sharp-toothed sharks are known from the Niobrara

190   Formation, and they have left an extensive record of tooth traces and shed teeth among other

191   vertebrates of the Smoky Hill Chalk Member (Everhart, 2005). The Niobrara species best known

192   for leaving bite traces is *Squalicorax kaupi*, but this identification can be excluded for the LACM

193   tooth because it lacks the asymmetrical crown, notched cutting edge and serrations

194   characterising the dentition of this genus (e.g. see Everhart, 2005; Becker & Chamberlain,

195   2012). The tooth is a good march for the large lamniform shark *Cretoxyrhina mantelli* (Fig. 3),

196   which has subtriangular, relatively broad, symmetrical and short crowns without serrated

197   margins (e.g. Shimada, 1997; Siverson & Lindgren, 2005, their fig 2; Bourdon & Everhart, 2011).

198   In particular, the morphology of the tooth in LACM 50926 matches teeth recovered from

199   anterior positions of *Cretoxyrhina* jaws (Shimada, 1997; Bourdon & Everhart, 2011, their figs 2,

200   5). The identification of the shark tooth as belonging to *Cretoxyrhina* was also independently

201   made by Konuki (2008) and Witton (2018). Comparison of the LACM tooth size with a superb *C.*

202   *mantelli* skeleton, FHSM VP-2187 (Shimada, 1997), suggests that the individual was c. 2.5 m

203   long. This is little more than one third of length of the largest known individuals of this species

204   (Everhart, 2005).

205

206   **Discussion:**

207   *Significance of association of* Pteranodon *and* Cretoxyrhina

208   Ecological interactions between pterosaurs and other species are rarely represented in

209   fossil specimens, despite vast increases in pterosaur specimen numbers in recent years (Witton,

210   2018). Data on diet from stomach contents is sparse, limited to a handful of taxa known to have

211   eaten fish (e.g. *Eudimorphodon* – Wild, 1978, *Pteranodon, Rhamphorhynchus* – Wellnhofer,

212   1991). Coprolites are also scarce, with only one record for pterosaurs known to date (Hone et

213   al., 2014). A number of animals are recorded as pterosaur consumers, including fish (e.g. Frey &

214   Tischlinger, 2012), dinosaurs (e.g. Hone et al., 2012), Crocodyliformes (Vremir et al., 2013) and

215   possibly plesiosaurs (Cicimurri & Everhart, 2001, although also see Witton, 2018), but they

216   remain very rare despite the good fossil records of these 'consumer' taxa. Thus, this additional

217   potential record of a pterosaur-carnivore association is significant.

218   The taphonomic history and association of LACM 50926 is unknown so it is difficult to

219   draw firm conclusions about the action that left the shark tooth in situ. However, we rule out

220   abiotic association of the pterosaur and shark tooth for several reasons: 1) embedded

221   *Cretoxyrhina* teeth and feeding traces are known from numerous Smoky Hill vertebrate fossils,

222   and are widely interpreted as related to feeding behaviour (Shimada, 1997; Everhart, 2004,

223   2005); 2) although isolated *Cretoxyrhina* teeth are common fossils in the Smoky Hill Chalk

224   Member (Everhart, 2005), its teeth have not been reported in association with any *Pteranodon*

225   fossils in the past, despite the large sample size of this pterosaur and the fact that other fish

226   remains (e.g. vertebrae) are not uncommonly associated with their remains (Bennett, 2001;

227   Hargrave, 2007); 3) the spatial relationship between the tooth and the vertebra is complex and

228   intimate, and unlike that expected to have occurred by chance association in a low energy

229   deposit such as the Niobrara Chalk. We thus prefer an interpretation of the tooth becoming

230   associated with the vertebra though the biting action of a small *Cretoxyrhina*.

231   We were unable to find additional indications of bite traces on LACM 50926. There is a

232   small and almost perfectly circular puncture on the neural arch of cervical four, behind the left

233   prezygapophysis but this is most likely a preparation trace or damage derived from a previous

234   museum mount. The damaged and missing neural spines of the cervical series may be linked to

235   the shark bite, but other pterosaur fossils show that these elements are prone to damage

236   and/or poor preservation, so other causes cannot be excluded.

237   *Cretoxyrhina* was a large (up to 7 m in length) and powerful carnivore, perhaps one of

238   the top predators of the Smoky Hill Chalk fauna (Everhart, 2005). Shimada (1997) compared its

239   likely ecological feeding guild to larger modern species of lamnid and carcharhinid sharks, and

240   there is fossil evidence that it consumed a variety of large vertebrates including mosasaurs,

241   plesiosaurs and large teleost fish (Shimada, 1997; Everhart, 2004, 2005). LACM 50926 is the first

242   palaeoecological link between this shark genus and a pterosaur however, this rarity perhaps

243   reflecting the relatively delicate nature of pterosaur skeletons against the evident bite force of

244   *Cretoxyrhina*. Extremely hollow bones such as those characterising most of the *Pteranodon*

245   skeleton are especially prone to failure against buckling forces (Currey, 2004) and likely broke

246   easily under strong bites from large predators.

247   Both Bennett (2001) and Hargrave (2007) have noted that *Pteranodon* may have been

248   consumed destructively by large aquatic carnivores, their relatively muscular torsos being

249   targeted, perhaps explaining why wing skeletons (which had considerably less soft-tissue, see

250   Bennett, 2008) are the most common form of associated pterosaur fossil in the Smoky Hill

251   Chalk Member. It should be noted however, that articulated wings are also common in the Late

252   Jurassic Solnhofen fauna where this may reflect decay and the loss of wings from intact and

253   floating corpses of pterosaurs (Beardmore, Lawlor & Hone, 2017), although this is not mutually

254   exclusive with the effects of predation and scavenging. Witton (2016) noted that, to date, only

255   the larger, more robust elements – limb bones and neck vertebrae – of larger pterosaur species

256   are known to preserve embedded teeth, and speculated that small pterosaurs and/or more

257   gracile pterosaur bones were probably too easily destroyed to record evidence of carnivore

258   bites. It may be that pterosaurs were not rare dietary components of *Cretoxyrhina* or other

259   animals, but that their anatomy precludes common fossilisation of evidence for these acts.

260   There is limited potential for knowing whether the LACM 50926 association reflects

261   predatory or scavenging behaviour from *Cretoxyrhina*. *Pteranodon* is widely considered to have

262   been a pelagic pterosaur species which foraged for small aquatic prey by means of dip-feeding,

263   fishing from an alighted position on the water surface or diving after food (Wellnhofer, 1991;

264   Bennett, 2001; Witton, 2013, 2016). Adaptations to aquatic launch (identified by Habib &

265   Cunningham, 2010) are apparent in *Pteranodon* and suggest that it may have routinely entered

266   (and thus needed to launch from) bodies of water. Thus, there are good reasons to think living

267   *Pteranodon* could have been within reach of predatory sharks, and the likely pterodactyloid

268   floating posture places their head and neck close to the waters' surface (Hone & Henderson,

269   2014). Various seabirds are known to be predated by pelagic predators, including sharks, in

270   modern times (Wetherbee, Cortés & Bizzarro, 2004; Johnson et al., 2006) and we cannot

271   exclude this possibility for the LACM *Pteranodon*. Witton (2018) noted that even moderately-

272   sized sharks, akin to the 2.5 m long *Cretoxyrhina* indicated by the LACM tooth, would vastly

273   outweigh the largest *Pteranodon* (35-50 kg – see Paul, 2002; Witton, 2008; Henderson, 2010 for

274   *Pteranodon* mass estimates), and we have little doubt that such predators could subdue these

275   pterosaurs if they caught them (Fig. 4). Conversely, *Pteranodon* likely had a relatively low body

276   density and their carcasses may have floated for sustained periods (Hone & Henderson, 2014).

277   This would make them obvious targets for scavenging marine animals. Ultimately, LACM 50926

278   preserves no evidence to falsify any of these hypotheses.

279   Evidence of the anacoracid shark *Squalicorax* consuming *Pteranodon* is known in the

280   Niobrara (e.g. KU 972 - KU, Kansas University, USA; YPM 2597, YPM 42810 – Bennett, pers.

281   comm. 06/16), and recent finds of Mooreville Chalk Formation *Pteranodon* also have bite marks

282   attributed to *Squalicorax kaupi* (RMM 3274 and ALMNH 8630) (Ehret & Harrell, 2018). This

283   body of evidence, augmented with the *Cretoxyrhina-Pteranodon* association described here,

284   and the recovery of fish remains within the gular region of *Pteranodon* specimens (Brown,

285   1943; Bennett, 2001, 2018) makes the trophic interactions of *Pteranodon* well understood

286   compared to most other pterosaurs (Witton, 2018). However, such finds are still relatively rare

287   occurrences - these seven associations are less than 1% of the >1100 specimens of *Pteranodon*

288   on record. In contrast, at least ten palaeoecologically significant fossil associations are known

289   for the Late Jurassic Solnhofen pterosaur *Rhamphorhynchus muensteri* (including five

290   associations with the carnivorous fish *Aspidorhynchus acutirostris* (e.g. Frey & Tishchlinger,

291   2012) and four examples of consumed items – see Witton, 2018 for a recent review). There are

292   perhaps 150 specimens of *Rhamphorhynchus* in public collections, suggesting that recording of

293   palaeoecological events is several times higher than in *Pteranodon* (>6%) despite a considerably

294   smaller sample size. The taphonomic factors contributing to this difference may be worthy of

295   further study.

296

297   **Acknowledgements:**

298   We thank Luis Chiappe and Maureen Walsh for access to the specimen and information on its

299   history and Stephanie Abramowicz for access to archival photographs of the specimen. We

300   would like to thank Steffi Klug for assistance on identification of the shark tooth, Dana Ehret

301   and Chris Bennett for discussions on the composite mount and bite marks on *Pteranodon* bones

302   and providing key literature. We thank both Dana Ehret and Chris Bennett for their reviews and

303   Mark Young for his handling of the manuscript as editor that helped improve this work.

304

305   **References:**

306   Acorn JH, Martin-Silverstone E, Glasier JR, Mohr S, Currie PJ. 2017. Response to Kellner (2017)

307   'Rebuttal of Martin-Silverstone, E., JRN Glasier, JH Acorn, S. Mohr, and PJ Currie, 2017'.

308   *Vertebrate Anatomy Morphology Palaeontology* 3.

309   Beardmore SR, Lawlor E, Hone DWE. 2017. Using taphonomy to infer differences in soft tissues

310   between taxa: an example using basal and derived forms of Solnhofen pterosaurs. *The*

311   *Science of Nature* 104:65.

312   Becker MA, Chamberlain JA. 2012. *Squalicorax* chips a tooth: a consequence of feeding-related

313   behavior from the lowermost Navesink Formation (Late Cretaceous: Campanian-

314   Maastrichtian) of Monmouth County, New Jersey, USA. *Geosciences* 2:109–129.

315   Bennett SC. 1991. Morphology of the Late Cretaceous pterosaur *Pteranodon* and systematics of

316   the Pterodactyloidea. Doctoral dissertation, University of Kansas, Systematics and Ecology.

317   Bennett SC. 1992. Sexual dimorphism of *Pteranodon* and other pterosaurs, with comments on

318   cranial crests. *Journal of Vertebrate Paleontology* 12:422–434

319   Bennett SC. 1993. The ontogeny of *Pteranodon* and other pterosaurs. *Paleobiology* 19:92–106

320   Bennett SC. 1994. Taxonomy and systematics of the Late Cretaceous pterosaur *Pteranodon*

321   (Pterosauria, Pterodactyloidea). *Occasional Papers of the Museum of Natural History,*

322   *University of Kansas, Lawrence* 169:1–70.

323   Bennett SC. 2001. The osteology and functional morphology of the Late Cretaceous pterosaur

324   *Pteranodon*. (parts 1 and 2). *Paleontographica Abteilung A*, 260:1–153.

325   Bennett SC. 2003. A survey of pathologies of large pterodactyloid pterosaurs. *Palaeontology*

326   46:185–198.

327   Bennett SC. 2018. New smallest specimen of the pterosaur *Pteranodon* and ontogenetic niches

328   in pterosaurs. *Journal of Paleontology* 92:254–271.

329   Bennett SC, Penkalski P. 2017. Waves of bone deposition on the rostrum of the pterosaur

330   *Pteranodon*. Geological Society of London, Special Publications, 455:69.

331   Bourdon J, Everhart MJ. 2011. Analysis of an associated *Cretoxyrhina mantelli* dentition from

332   the Late Cretaceous (Smoky Hill Chalk, Late Coniacian) of western Kansas. *Transactions of*

333   *the Kansas Academy of Science* 114:15–32.

334   Bramwell CD, Whitfield GR. 1974. Biomechanics of *Pteranodon*. *Philosophical Transactions of*

335   *the Royal Society of London: Series B* 267:503–581.

336   Brandão RS, Rodrigures T. 2018. Reappraisal of *Dawndraco kanzai* as a valid taxon. *Flugsaurier*

337   *2018 conference abstracts*, 17.

338   Brown B. 1943. Flying reptiles. *Natural History* 52:104–111.

339   Carpenter K. 2008. Vertebrate biostratigraphy of the Smoky Hill Chalk (Niobrara Formation) and

340   the Sharon Springs Member (Pierre Shale). In: Harries PJ. ed. *High-Resolution Approaches in*

341   *Stratigraphic Paleontology: Topics in Geobiology Series,* 21:421–437.

342   Cicimurri DJ, Everhart MJ. 2001. An elasmosaur with stomach contents and gastroliths from the

343   Pierre Shale (Late Cretaceous) of Kansas. *Transactions of the Kansas Academy of Science*

344   104:129–143.

345   Eaton GF. 1910. Osteology of *Pteranodon*. *Memoirs of the Connecticut Academy of Arts and*

346   *Sciences* 2:1–38.

347   Ehret DJ, Harrell Jr, TR. 2018. Feeding traces on a Pteranodon (Reptilia: Pterosauria) bone from

348   the Late Cretaceous (Campanian) Mooreville Chalk in Alabama, USA. Palaios, 33:414-418.

349   Everhart MJ. 2004. Late Cretaceous interaction between predators and prey. Evidence of

350   feeding by two species of shark on a mosasaur. *PalArch, vertebrate palaeontology*

351   *series* 1:1–7.

352   Everhart MJ. 2005. *Oceans of Kansas*. Indiana University Press.

353   Frey E, Tischlinger H. 2012. The Late Jurassic Pterosaur *Rhamphorhynchus*, a frequent victim of

354   the ganoid fish *Aspidorhynchus*? *PLoS ONE* 7:e31945.

355   Habib M, Cunningham J. 2010. Capacity for water launch in *Anhanguera* and *Quetzalcoatlus*.

356   A*cta Geoscientica Sinica* 31:24–25.

357   Hankin EH, Watson DMS. 1914. On the flight of pterodactyls. *The Aeronautical Journal* 18:324-

358   335.

359   Hargrave JE. 2007. *Pteranodon* (Reptilia: Pterosauria): Stratigraphic distribution and taphonomy

360   in the lower Pierre Shale Group (Campanian), western South Dakota and eastern Wyoming.

361   In: Martin JE, Parris DC. eds. *The Geology and Paleontology of the Late Cretaceous Marine*

362   *Deposits of the Dakotas: Geological Society of America Special Paper* 427:215–225.

363   Hattin DE. 1982. Stratigraphy and depositional environment of Smoky Hill Chalk Member,

364   Niobrara Chalk (Upper Cretaceous) of the type area, western Kansas. *Kansas Geological*

365   *Survey Bulletin* 225:108.

366   Henderson DM. 2010. Pterosaur body mass estimates from three-dimensional mathematical

367   slicing. *Journal of Vertebrate Paleontology* 30:768–785.

368   Hone DWE, Henderson DM. 2014. The posture of floating pterosaurs: ecological implications for

369   inhabiting marine and freshwater habitats. *Palaeogeography, Palaeoclimatology,*

370   *Palaeoecology* 398:89–98.

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

372   dromaeosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 331:27–30.

373   Hone DWE, Henderson DM, Therrien F, Habib MB. 2015. A specimen of *Rhamphorhynchus* with

374   soft tissue preservation, stomach contents and a putative coprolite. *PeerJ* 3:e1191.

375   Johnson RL, Venter A, Bester MN, Oosthuizen WH. 2006. Seabird predation by white shark,

376   *Carcharodon carcharias*, and Cape fur seal, *Arctocephalus pusillus pusillus*, at Dyer

377   Island. *South African Journal of Wildlife Research* 36:23–32.

378   Kellner AWA. 2010. Comments on the Pteranodontidae (Pterosauria, Pterodactyloidea) with

379   the description of two new species. *Anais de Academia Brasileira de Ciencias* 82:1063–

380   1084.

381   Konuki Reira. 2008. Biostratigraphy of Sea Turtles and Possible Bite Marks on a *Toxochelys*

382   (Testudine, Chelonioidea) from the Niobrara Formation (Late Santonian), Logan County,

383   Kansas, and Paleoecological Implications for Predator-prey Relationships Among Large

384   Marine Vertebrates. Masters dissertation, Fort Hays State University,

385   Marsh OC. 1876. Notice of a new sub-order of Pterosauria. *American Journal of Sciences*

386   11:507–509.

387   Martin-Silverstone E, Glasier JRN, Acorn JH, Mohr S, Currie PJ. 2017. Reassessment of

388   *Dawndraco kanzai* Kellner, 2010 and reassignment of the type specimen to *Pteranodon*

389   *sternbergi* Harksen, 1966. *Vertebrate Anatomy Morphology Palaeontology* 3:47–59.

390   Paul GS. 2002. *Dinosaurs of the air: the evolution and loss of flight in dinosaurs and birds*. JHU

391   Press.

392   Shimada K. 1997. Paleoecological relationships of the Late Cretaceous lamniform shark,

393   *Cretoxyrhina mantelli* (Agassiz). *Journal of Paleontology* 71:926–933.

394   Siverson M. Lindgren J. 2005. Late Cretaceous sharks *Cretoxyrhina* and *Cardabiodon* from

395   Montana, USA. *Acta Palaeontologica Polonica* 50:301–314.

396   Stein RS. 1975. Dynamic analysis of *Pteranodon ingens*: a reptilian adaptation to flight. *Journal*

397   *of Paleontology* 49:534–548.

398   Vremir M, Kellner AW, Naish D, Dyke GJ. 2013. A new azhdarchid pterosaur from the Late

399   Cretaceous of the Transylvanian Basin, Romania: implications for azhdarchid diversity and

400   distribution. *PLoS One* 8:e54268.

401   Wellnhofer P. 1991. The Illustrated Encyclopedia of Pterosaurs. Salamander Books, London.

402   Wetherbee BM, Cortés E, Bizzarro JJ. 2004. Food consumption and feeding habits. *Biology of*

403   *Sharks and their Relatives*, 225–246.

404   Wild R. 1978. Die Flugsaurier (Reptilia, Pterosauria) aus der Oberen Trias von Cene bei

405   Bergamo, Italien. *Bollettino della Società Paleontologica Italiana* 17:176–-256

406   Witton MP. 2008. A new approach to determining pterosaur body mass and its implications for

407   pterosaur flight. *Zitteliana B* 28:143–158.

408   Witton MP. 2010. *Pteranodon* and beyond: the history of giant pterosaurs from 1870 onwards.

409   *Geological Society, London, Special Publications* 343:313–323.

410   Witton MP. 2013. *Pterosaurs: natural history, evolution, anatomy*. Princeton University Press.

411   Witton MP. 2018. Pterosaurs in Mesozoic food webs: a review of fossil evidence. *Geological*

412   *Society, London, Special Publications* 455:7–23.

413   Witton MP, Habib M. 2010. On the size and flight diversity of giant pterosaurs, the use of birds

414   as pterosaur analogues and comments on pterosaur flightlessness. *PLoS ONE* 5:e13982.

415

416   Figure captions.

417

418   Fig 1. A, mounted *Pteranodon* sp. skeleton LACM 50926 on display in the Los Angeles county

419   museum with highlighted section of the vertebrae shown below; B, Close up of the

420   vertebral series and shark tooth (indicated by an arrow). Cervical vertebrae III-VII as

421   mounted on the display are indicated. Scale bar is 50 mm – this is an approximate value

422   based on published measurements of the vertebrae. Image credit: A, Stephanie

423   Abramowicz, courtesy Dinosaur Institute, Natural History Museum of Los Angeles County,

424   B, David Hone.

425

426   Fig 2. Two close up views of the *Cretoxyrhina mantelli* tooth with tracings. A, left dorsolateral

427   view; B, left dorsoventral view showing its intimate association with cervical vertebra IV.

428   The tooth is highlighted in medium grey, the 4th cervical vertebra in pale grey and the 5th

429   cervical in dark grey. Abbreviations: ns neural spine, prz prezygopophysis, psz

430   postzygopophysis, st shark tooth. Image credit: David Hone.

431

432   Fig 3. Tracing of *Cretoxyrhina mantelli* anterior teeth from Bourdon and Everhart (2011, their fig

433   5, mirrored from their original). A, position 3 in the jaw; B, position 4; C, LACM 50926

434   tooth. The roots of the teeth are shaded in pale grey and the enamel is dark grey. Image

435   credit: David Hone.

436

437   Fig. 4. Life reconstruction of a c. 2.5 m long breaching *Cretoxyrhina mantelli* biting the neck of a

438   5 m wingspan *Pteranodon longiceps*, a scene inspired by LACM 50926. The predatory

439   behaviour of this scene is speculative with respect to the data offered by the specimen, but

440   reflects the fact that *Cretoxyrhina* is generally considered a predatory species, the vast

441   weight advantage of the shark against the pterosaur (see text), and the juvenile impulse of

442   the artist to draw an explosive predatory scene. Image credit: Mark Witton.

Figure 1

Mounted Pteranodon and close up of the neck

Fig 1. A, mounted *Pteranodon* sp. skeleton LACM 50926 on display in the Loa Angeles county museum with highlighted section of the vertebrae shown below; B, Close up of the vertebral series and shark tooth (indicated by an arrow). Cervical vertebrae III-VII are indicated. Scale bar is 50 mm – this is an approximate value based on published measurements of the vertebrae. Image credit: A, Stephanie Abramowicz, courtesy Dinosaur Institute, Natural History Museum of Los Angeles County, B, David Hone.
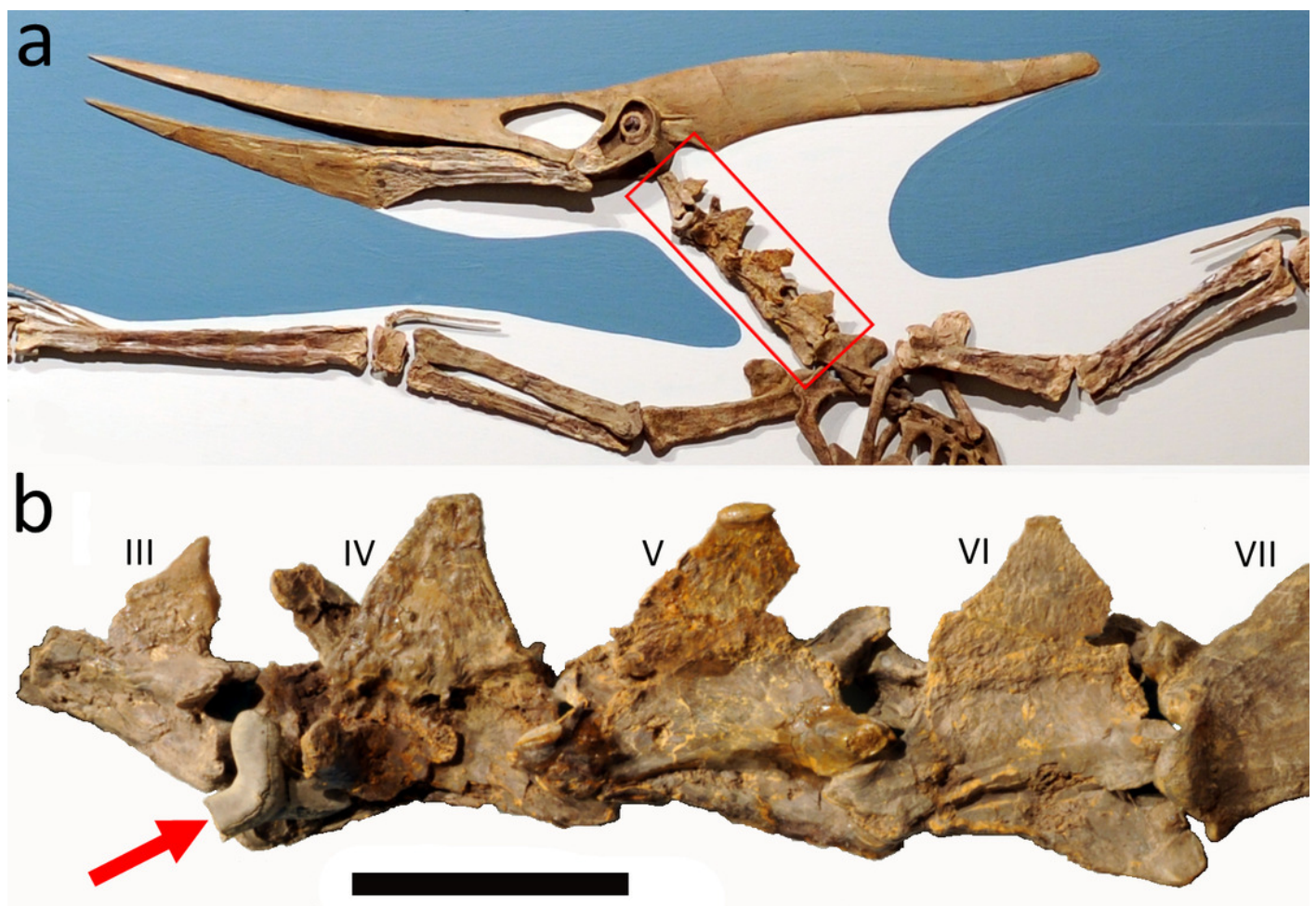
Figure 2

Two close up views of the *Cretoxyrhina mantelli* tooth with tracings.

Fig 2. Two close up views of the *Cretoxyrhina mantelli* tooth with tracings. A, left dorsolateral view; B, left dorsoventral view showing its intimate association with cervical vertebra IV. The tooth is highlighted in medium grey, the 4th cervical vertebra in pale grey and the 5th cervical in dark grey. Abbreviations: ns neural spine, prz prezygopophysis, psz postzygopophysis, st shark tooth. Image credit: David Hone.
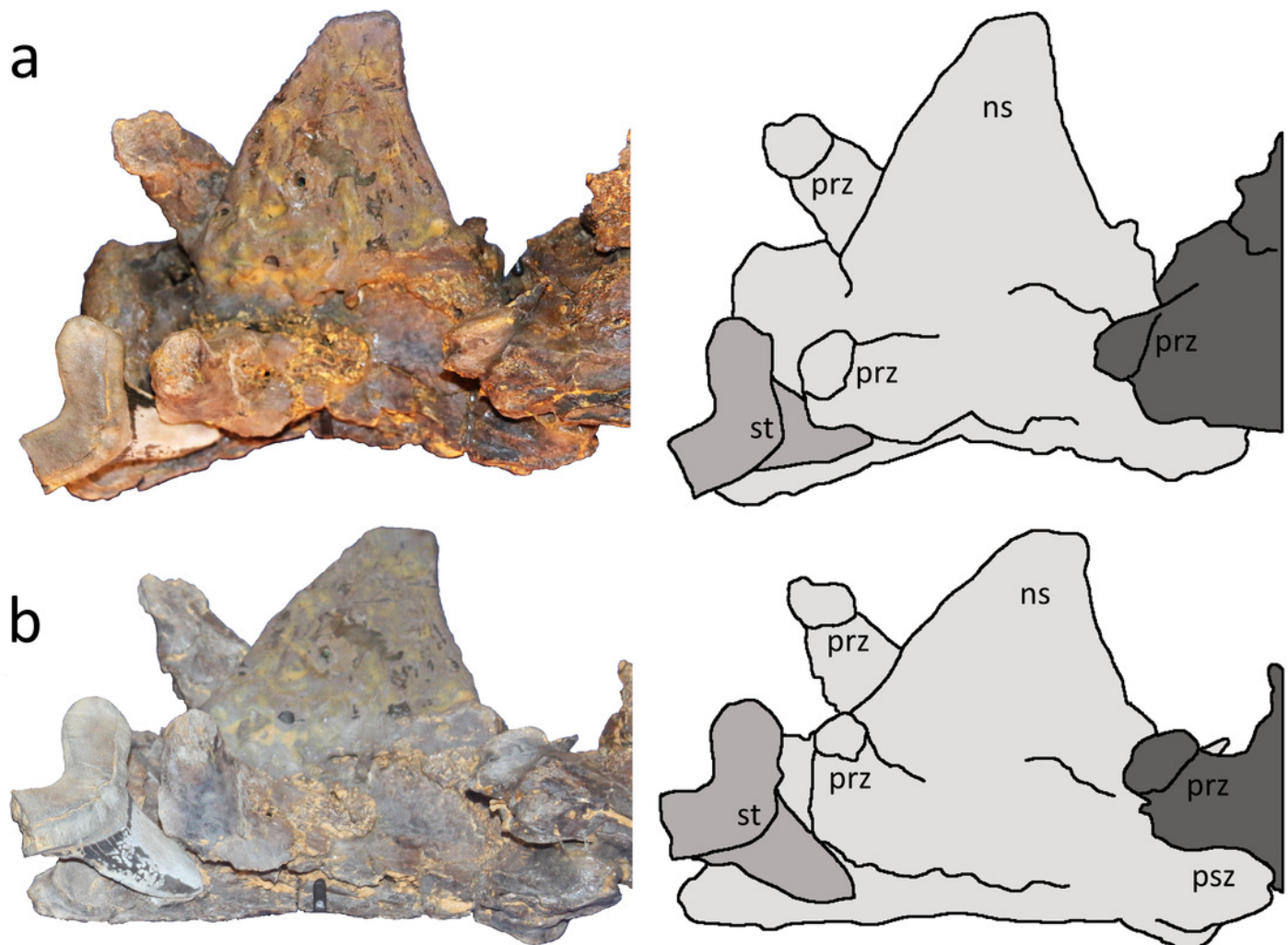
Figure 3

Cretoxyrhina mantelli anterior teeth

Fig 3. Tracing of *Cretoxyrhina mantelli* anterior teeth from Bourdon and Everhart (2011, their fig 5, mirrored from their original). A, position 3 in the jaw; B, position 4; C, LACM 50926 tooth. The bases of the teeth are shaded in pale grey and the enamel is dark grey. Image credit: David Hone.
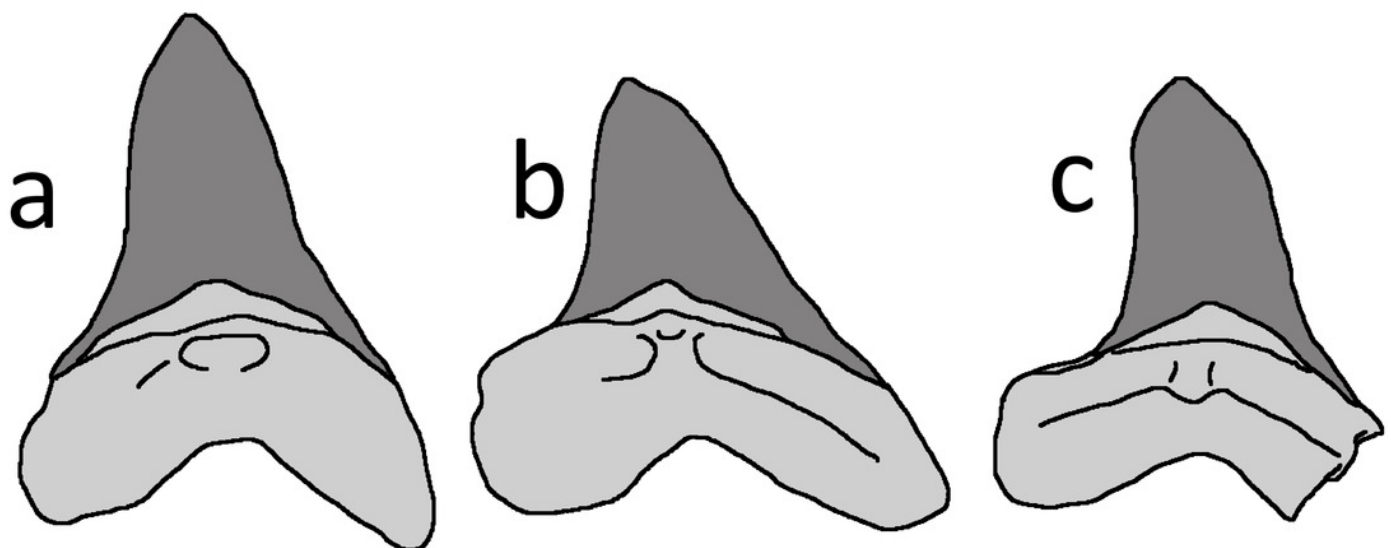
Figure 4

Life reconstruction of a *Cretoxyrhina mantelli* attacking a *Pteranodon longiceps*

Fig. 4. Life reconstruction of a c. 2.5 m long breaching *Cretoxyrhina mantelli* biting the neck of a 5 m wingspan *Pteranodon longiceps*, a scene inspired by LACM 50926. The predatory behaviour of this scene is speculative with respect to the data offered by the specimen, but reflects the fact that *Cretoxyrhina* is generally considered a predatory species, the vast weight advantage of the shark against the pterosaur (see text), and the juvenile impulse of the artist to draw an explosive predatory scene. Image credit: Mark Witton.