Comments by S. Christopher Bennett on the manuscript "Evidence for the Cretaceous shark *Cretoxyrhina mantelli* feeding on the pterosaur *Pteranodon*" by D.W. E. Hone, M. P. Witton, and M. B. Habib.

The manuscript describes a tooth of the lamnid shark *Cretoxyrhina* preserved in association with cervical vertebrae of *Pteranodon*. Well written, reasonable conclusions. Not earth-shatteringly important, but worthy of publication.

Numbered Comments

The numbered comments below refer to the circled numbers that I have placed in the right margin of the manuscript, and the comments are written as directed to the authors.

1 - I don't like this construction and I would write as something like "argued that Niobrara pteranodontids comprised..."

2 - If the mounted skeleton was really from a single individual, it would be one of the most complete *Pteranodon* specimens ever found. It is quite likely that it consists of multiple individuals. One ulna has written on its back "Left ulna (Extra)". Note also that the alternate number of the mandible is a Locality number, which if correctly read as 65218 corresponds to LACM 50927 (50926 is from Loc. #65216), which includes a femur, distal end of the other femur, and the proximal end of a coracoid. Lastly, there is LACM 51132, consisting of an ulna, incomplete MCIV, and complete P1 - P4, which I did not see or measure in July 1986, but was noted on the card as "On display." Perhaps it was on display as part of the composite.

3 - If I remember correctly, Brown, B. 1904. Stomach stones and food of plesiosaurs. Science. N. S., 19 or 20:184-185 reports on *Pteranodon* in plesiosaur stomach contents.

4 - There may be a significant difference between floating corpses in the Western Interior Seaway and those in Solnhofen lagoons in that the waters in the Seaway presumably were always hospitable whereas I am under the impression that at times the waters in the lagoons were inhospitable such that predators and scavengers would have been absent.

5 - Bennett (2018 - smallest *Pteranodon* paper) described and illustrated the AMNH specimen that preserves a bolus of fish vertebrae and mentions a second specimen with a bolus.

6 - I am aware that I have used different numbers in different papers, but I try to be consistent within papers. It bothers me that you used "well over 1000" in line 33 and ">1100" here even though the two statements are logically consistent.

7 - Note that Unwin in his *Deep Time* book states in a table that there are something like 3 or 6000 *Rhamphorhynchus* specimens; I can't find my copy right now and am writing from fallible memory.

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

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Abstract:

Here we describe a specimen of the large, pelagic pterodactyloid pterosaur *Pteranodon* sp. that shows the tooth of a large lamniform shark, *Cretoxyrhina mantelli*, associated with a cervical vertebra. Though the tooth does not pierce the vertebral periosteum the intimate association of the fossils – in which the tooth is wedged below the left prezygopophysis – suggests their association was not mere chance, and we interpret the association as evidence of *Cretoxyrhina* biting the pterosaur. There are several records of *Pteranodon* having been consumed by 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 *Pterandon* 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.

Introduction:

Pteranodon is a large pterodactyloid pterosaur from the Late Cretaceous (Coniacian-Campanian) of North America with an estimated maximum wingspan of 7.25 m (Bennett, 2001). The genus was among the first pterosaurs reported from North America (Marsh, 1876 – see Bennett, 2001 and Witton, 2010 for context of its discovery) and has become one of the best known flying reptiles thanks to a representation of well over 1000 specimens – the highest sample size for any pterosaur genus. Although most specimens are incomplete and crushed, every component of its osteology is known and has been described in detail (Eaton, 1910; Bennett, 1991, 1994, 2001, 2017, 2018; Bennett & Penkalski, 2018). As a result of the number of available specimens, its long research history and comprehensive documentation, the genus has become a cornerstone of pterosaur research and one of the most completely understood flying reptiles. *Pteranodon* has been an important animal for understanding pterosaur flight (Hankin & Watson, 1914; Bramwell & Whitfield, 1974; Stein, 1975), the evolution of giantism in flying animals (Witton & Habib, 2010), ~~as well as~~ pterosaur ontogeny (Bennett, 1993), and palaeoecology (Bennett, 2001; Witton, 2018).

The majority of *Pteranodon* specimens are known from the Late Cretaceous Niobrara Formation from Kansas, U.S.A., a marine deposit created by the Western Interior Seaway, though other specimens also occur in additional formations in Wyoming and South Dakota (Bennett, 1994, 2001). Niobrara specimens of *Pteranodon* occur in localities that were hundreds of kilometres from the palaeocoastline and this, along with a number of aspects of functional anatomy, has seen the genus long interpreted as a seagoing, pelagic animal (e.g., Bennett, 2001; Witton, 2013, p. 179).

Pteranodon was likely an important component of the Western Interior Seaway ecosystem. It seems to have been relatively abundant, being known from both a large number of fossils and making up some 97% of Niobrara Formation pterosaur finds. It was also a large animal - Bennett (1993) identified a bimodal size distribution among the large *Pteranodon* sample where two thirds of individuals were c. 3.5 m in wingspan, and the remaining third were much larger, some exceeding 7 m across the wings (Bennett, 2001). Larger specimens likely exceed the masses of any flying bird, extant or extinct, with estimated body masses of 35-50 kg

largest Niobrara specimen = ~6.25 m

for animals of 6 m wingspan (Paul, 2002; Witton, 2008; Henderson 2010), compared to 21.9–40.1 kg in the largest fossil flying birds, the pelagornithids (Mayr & Rubilar-Rogers, 2010; Ksepka, 2014). *Pteranodon* populations may therefore have been major consumers in the Western Interior Seaway ecosystem, as well as potentially sources of food for other animals.

However, our understanding of interactions between *Pteranodon* and other taxa of the Seaway is limited. As with other pterosaur species, few *Pteranodon* fossils preserve remains of ingested content and they only rarely preserve evidence of consumption by other animals (Witton, 2018). Moreover, documentation of its palaeoecological data has not comprehensive. Regurgitated fish gut content is preserved in the gular region of one *Pteranodon* specimen (Brown, 1943; Bennett, 2001, 2018) and some palaeoecological significance has been ascribed to small fish vertebrae found in association with *Pteranodon* fossils (Bennett, 2001; Hargrave, 2007; Ehret, Harrell & Ebersole, 2015). Biting traces on *Pteranodon* elements, both briefly described (Ehret, Harrell & Ebersole, 2015) and undescribed, suggest some individuals were eaten by the anacoracid shark *Squalicorax kaupi* as well as other unidentified carnivores (Witton, 2018). The record of pterosaur ecological interactions is sufficiently sparse that any fossilised interactions with other species should be put on record, so we hereby report on a series of *Pteranodon* cervical vertebrae, LACM 50926, associated with a tooth of the lamniform shark *Cretoxyrhina mantelli*. This is first documented occurrence of this large shark interacting with any pterosaur.

Systematic nomenclature:

The taxonomy of *Pteranodon* is a matter of recent dispute. For the last two decades most workers have followed the treatment of the genus outlined by Bennett (1994), who made a case for reducing the 11 binomials associated with *Pteranodon* (excluding those names related to *Nyctosaurus*) to two sexually dimorphic chronospecies: the older *Pteranodon sternbergi* and the younger *P. longiceps*. In this scheme, the skulls of these species are distinguished by details of their cranial crests, and (more tentatively) occiput orientation and mandibular ramus depth. Postcranial bones of these specimens are near identical and of little taxonomic utility (Bennett, 1994). More recently, Kellner (2010) argued for *Pteranodon sensu* Bennett (1994) being comprised of four species in three genera. While agreeing with Bennett (1994) that all 'historic' *Pteranodon* species were problematic excepting *longiceps* and *sternbergi*, Kellner (2010) created a multi-taxic pteranodontid assemblage for the Niobrara specimens comprising *Pteranodon longiceps*, *Geosternbergia* (rather than *Pteranodon*) *sternbergi*, and two novel species, *Geosternbergia maiseyi* and *Dawndraco kanzai*. These taxa are primarily distinguished by headcrest morphology and details of the posterior skull, as well as finer stratigraphic divisions of the Niobrara Formation (Kellner, 2010) than the broader 'upper' and 'lower' divisions of the Smoky Hill Chalk *Pteranodon* fauna recognised by other workers (e.g. Bennett, 1994; Everhart, 2005; Carpenter, 2008). Subsequent criticism of this proposal has questioned the validity of the proposed differences between at least *Dawndraco* and *Pteranodon* sensu lato, noted incongruence between the stratigraphic divisions signified by Kellner (2010) against other Niobrara Formation taxa, as well as the lack of statistical support for splitting *Pteranodon* into multiple genera, compared to the strong statistical support for Bennett's interpretation (Martin-Silverstone et al., 2017; Acorn et al., 2017). We thus follow several other works (Witton, 2013, 2018; Bennett 2016, 2017, 2018) in retaining Bennett's (1994) treatment of *Pteranodon* here. Note however that discussion of *Pteranodon* taxonomy is ongoing (Brandão & Rodrigues, 2018). ← That talk was hilarious!

Materials and Methods:

LACM 50926 (Los Angeles County Museum of Natural History, USA) is specimen of *Pteranodon* mounted in a large glass case for public display at the Los Angeles County Museum for Natural History and is unfortunately difficult to access directly (Fig 1). The specimen has a large *Cretoxyrhina mantelli* tooth intimately associated with the fourth cervical vertebra (Fig 2). Parts of the mount are genuine fossils and these are well preserved (showing only limited crushing compared to many specimens of the genus). However, several elements are reconstructed to replace missing parts and the mount composites material from at ~~least two~~ several individuals (see Bennett, 1991, 2001): size discrepancy between some neighbouring elements also suggests at least one more individual may be incorporated. Bennett (pers. comm. 6/ 2016) also notes material accessioned under this number (much of it in collections space and not in the exhibit mount) includes three mandibular rami, confirming the multi-individual nature of this specimen. An alternate specimen number (65218) occurs on the mandible and the cervical bearing the shark tooth, but this cannot be seen on other elements. This may indicate that the mandible and cervical were associated when discovered. Bennett (2001) was able to identify many of the LACM 50926 forelimb elements as belonging to a single individual, although there are no records to indicate which parts of the mounted specimen might relate directly to the cervical series. The preservation quality and size of the vertebrae correspond well to the other

(2)

elements (including the forelimb bones) and this implies that LACM 50926 may represent a partial or nearly complete skeleton. However, the absence of both anteriormost and posterior cervical vertebrae means no anatomical continuity links the 50926 vertebrae with the rest of the material, and their association to the rest of the skeleton cannot be confidently assumed.

Notes held at the LACM show that the specimen was collected in 1965 by M.C. Bonner from Niobrara Chalk 23, Niobrara Formation, Logan County, Kansas. Bennett (1991) refers to two specimens under this number (LACM 50926 and 50926 "A") and concurs with this locality, adding that they were collected between Marker Units 14 and 19. This makes a Santonian age likely for LACM 50926 (Hattin, 1982; Bennett, 1994).

Description:

The anatomy of *Pteranodon* has been described in detail elsewhere (Bennett, 2001) and we will therefore focus exclusively on the association between the shark tooth and pterosaur material. The cervical vertebra bearing the shark tooth is preserved in contact with two other cervicals as a series of three elements. Thus, within the composite context of the LACM specimen, these vertebrae at least can be safely considered part of a single individual. The cervicals are preserved in articulation with contact between the successive post- and prezygopophyses. These are identified by Bennett (2001) as cervical vertebrae 4-6, and he also identified a preceding, though not articulated, cervical in the LACM 50926 mount as a cervical 3. The vertebrae retain some three-dimensionality, although they are somewhat crushed at an oblique angle, shearing them along their midline such that the left sides are depressed and right sides elevated (Figs 1-2). The neural spine is missing (now restored) from cervical 4 and parts of

see lines 231-2 and 424

the neural spines cervicals 5 and 6 are damaged. Damage to the bone cortex reveals the internal structure of the bones in all three vertebrae.

The centrum lengths of the three cervical vertebrae in the series have been measured as 69.0, 77.8, and 71.5 mm respectively (Bennett, 2001). Based on comparisons to other specimens this would correspond to a *Pteranodon* with a c. 5 m wingspan, and was presumably therefore osteological adult or near adult in size. The embedded shark tooth is approximately 24 mm long (this was measured from photographs as it was impossible to measure the tooth given its location and the mount of the specimen), subtriangular in shape and highly compressed labiolingually. A wide, lunate root is formed from two obtusely angled, swollen root lobes. The termination of the left lobe (viewed from lingual aspect) forms a broad, somewhat rounded surface, but the termination of the right lobe is missing (Fig. 2). The crown is swollen on the labial surface, c. 12 mm long (measured from the apex of the root to apex of the crown), almost symmetrical but not significantly recurved with respect to the root. The tooth appears to lack serrations but the lateral and medial crown edges are somewhat worn with chipped margins. The tooth enamel is bright white with grey to brown patches, and the base of the tooth is pale grey-brown and close in colour to that of the pterosaur elements.

The tooth lies between the left prezygopophysis of cervical 4 and the centrum. In some aspects it appears that the tooth is wedged or has cut into the base of the prezygopophysis and the centrum; however, it lies medial to the prezygopophysis and does not contact it directly. The tooth is at preserved at a shallow angle to the long axis of the vertebra, (though this may reflect the crushing of the specimen rather than its original orientation) and the crown apex faces posteriorly and ventrally with respect to the vertebral corpus. The tip of the tooth does appear to penetrate the centrum but the tip of the tooth contacts it.

Results:

Taxonomic identities:

The composite nature of LACM 50926 complicates discussions of its affinities, but there is no doubt that the specimen can be referred to *Pteranodon* given its provenance and matching anatomy to this pterosaur (Eaton, 1910; Bennett, 2001). Identification to species level is more problematic as *Pteranodon* taxonomy is exclusively informed by the posterior skull region (e.g. Eaton, 1910; Bennett, 1994; Kellner, 2010), and the vertebra is not associated with any skull material. Following Bennett's (1994) tentative suggestion that *P. sternbergi* may have a shallower mandible than *P. longiceps* we compared the LACM 50926 mandibular ramus with specimens referred to these species. However, we were unable to determine a significant match with either taxon. Hargrave (2007) suggested that the tomial margins of posterior *P. longiceps* mandibles are curved, and this morphology is present in the LACM 50926 mandible. However, while we agree this can be seen in some *P. longiceps* (e.g. YPM 2594 - YPM, Yale Peabody Museum, USA) it does not seem to be a universal trait (e.g. YPM 1177).

The recovery of LACM 50926 from marker units 14-19 of Hattin's (1982) Smoky Hill Chalk stratigraphy suggests it pertains to younger Niobrara beds yielding *Pteranodon longiceps* rather than *P. sternbergi* (Bennett, 1994; Carpenter, 2008, although Kellner, 2010 argues that species more closely related to *P. sternbergi* than *P. longiceps* may persist into younger deposits) and this indicates LACM 50926 probably represents *P. longiceps*. In lieu of diagnostic fossil material however, we treat the specimen as *Pteranodon* sp.

A number of medium- to large-sized, sharp-toothed sharks are known from the Niobrara Formation, and they have left an extensive record of tooth marks and shed teeth among other vertebrates of the Smoky Hill Chalk Member (Everhart, 2005). The Niobrara species particularly best known for this behaviour is *Squalicorax kaupi*, but this identification can be excluded for the LACM tooth because it lacks the asymmetrical crown, notched cutting edge and serrations characterising the dentition of this genus (e.g. see Everhart, 2005; Becker & Chamberlain, 2012). The tooth is a good march for the large lamniform shark *Cretoxyrhina mantelli* (Fig. 3), which has subtriangular, relatively broad and short crowns without serrated margins, and are not recurved (e.g. Schimada, 1997; Siverson & Lindgren, 2005, their fig 2; Bourdon & Everhart, 2011). In particular, the morphology of the tooth in LACM 50926 matches teeth recovered from anterior positions of *Cretoxyrhina* jaws (Schimada, 1997; Bourdon & Everhart, 2011, their figs 2, 5). This identification of the shark tooth here as belonging to *Cretoxyrhina* was also independently made by Konuki (2008). Comparison of the LACM tooth size with a superb *C. mantelli* skeleton, FHSM VP-2187 (Schimada, 1997), suggests that the shark individual was c. 2.5 m long. This is little more than one third of length of the largest known individuals of this species.

Discussion:

Significance of association of Pteranodon *and* Cretoxyrhina

Ecological interactions between pterosaurs and other species are rarely represented in fossil specimens, despite vast increases in pterosaur specimen numbers in recent years (Witton, 2018). Data on diet from stomach contents is sparse, limited to a handful of taxa known to have eaten fish (e.g. *Eudimorphodon* – Wild, 1978, *Pteranodon, Rhamphorhynchus* – Wellnhofer, 1991). Coprolites are also scarce, with only one record for pterosaurs known to date (Hone et al., 2014). A number of animals are recorded as pterosaur consumers, including fish (e.g. Frey & Tischlinger, 2012), dinosaurs (e.g. Hone et al., 2012), Crocodyliformes (Vremir et al., 2013) and possibly plesiosaurs (Cicimurri & Everhart, 2001, but also see Witton, 2018), but they remain very rare fossils, despite the good fossil records of these 'consumer' taxa. Thus, this additional potential record of a pterosaur-carnivore association is significant. (3)

The taphonomic history and association of LACM 50926 is unknown so it is difficult to draw firm conclusions about the action that left the shark tooth in situ. However, we rule out abiotic association of the shark and pterosaur tooth for several reasons: 1) embedded *Cretoxyrhina* teeth and feeding traces are known from numerous Smoky Hill vertebrate fossils, and are widely interpreted as related to feeding behaviour (Shimada, 1997; Everhart, 2004, 2005); 2) although isolated *Cretoxyrhina* teeth are common fossils in the Smoky Hill Chalk Member (Everhart, 2005), its teeth have not been reported in association with any *Pteranodon* fossils in the past, despite the large sample size of this pterosaur and the fact that other fish remains (e.g. vertebrae) are not uncommonly associated with their remains (Bennett, 2001; Hargrave, 2007); 3) the spatial relationship between the tooth and the vertebra is complex and intimate, and unlike that expected to have developed by chance in a low energy deposit such as the Niobrara Chalk. We thus prefer an interpretation of the tooth being associated with the vertebra when as the remnant of a bite from a small *Cretoxyrhina*.

We were unable to find additional indications of bite marks or feeding traces on LACM 50926. There is a small and almost perfectly circular puncture on the neural arch of cervical four, behind the left prezygopohysis but this is most likely a preparation mark or damage derived from a previous museum mount. The damaged and missing neural spines of the cervical series may be linked to the shark bite, but other pterosaur fossils show that these elements are prone to damage and/or poor preservation, so other causes cannot be excluded.

Cretoxyrhina was a large (up to 7 m in length) and powerful carnivore, perhaps one of the top predators of the Smoky Hill Chalk fauna (Everhart, 2005). Shimada (1997) compared its likely ecological feeding guild to larger modern species of lamnid and carcharhinid sharks, and there is fossil evidence that it consumed a variety of large vertebrates including mosasaurs, plesiosaurs and large teleost fish (Schimada, 1997; Everhart, 2004, 2005). LACM 50926 is the first palaeoecological link between this shark genus and a pterosaur. The remains of large aquatic vertebrates bitten by *Cretoxyrhina* may be marked by not only shed teeth and tooth gouges but also shorn and broken bones, and its teeth are often chipped from the force of impacting animal skeletons. These are indications of a powerful bite, and the rarity of pterosaur-*Cretoxyrhina* associations may reflect the relatively delicate nature of pterosaur skeletons against the evident bite strength of this shark. Extremely hollow bones such as those characterising most of the *Pteranodon* skeleton are especially prone to failure against buckling forces (Currey, 2004) and likely broke easily under strong bites from large predators.

Both Bennett (2001) and Hargrave (2007) have noted that *Pteranodon* may have been consumed destructively by large aquatic carnivores, their relatively muscular torsos being targeted and perhaps explaining why wing skeletons (which had considerably less soft-tissue, see Bennett, 2008) are the commonest form of associated pterosaur fossil in the Smoky Hill Chalk Member. It should be noted however, that articulated wings are also common in the Late Jurassic Solnhofen fauna where this is interpreted to be a result of decay and the loss of wings from intact and floating corpses of pterosaurs (Beardmore, Lawlor & Hone, 2017), although this is not mutually exclusive with the effects of predation and scavenging. Witton (2016) noted that, to date, only the larger, more robust elements of larger pterosaur species – limb bones and neck vertebrae – are known to preserve embedded teeth, and speculated that small pterosaurs and/or more gracile pterosaur bones were probably too easily destroyed to record evidence of carnivore bites. It may be that pterosaurs were not rare dietary components of *Cretoxyrhina* or other animals, but that their anatomy precludes common fossilisation of evidence for these acts.

There is limited potential for knowing whether the LACM 50926 association reflects a predatory or a scavenging act. *Pteranodon* is widely considered to have been a pelagic pterosaur species which foraged for small aquatic prey by means of dip-feeding, fishing from an alighted position on the water surface or diving after food (Wellnhofer, 1991; Bennett, 2001; Witton, 2013, 2016). Adaptations to aquatic launch (identified by Habib & Cunningham, 2010) are apparent in *Pteranodon* and suggest that it may have routinely entered (and thus needed to launch from) bodies of water. There are thus good reasons to think living *Pteranodon* could have been within reach of predatory sharks, and the likely pterodactyloid floating posture places their head and neck close to the waters' surface (Hone & Henderson, 2014). Various seabirds are known to be predated by pelagic predators, including sharks, in modern times (Wetherbee, Cortés & Bizzarro, 2004; Johnson et al., 2006) and we cannot exclude this possibility for the LACM *Pteranodon*. Witton (2016) noted that even moderately-sized sharks akin to the 2.5 m long *Cretoxyrhina* indicated by the LACM tooth would vastly outweigh the largest *Pteranodon* (35-50 kg – see Paul, 2002; Witton, 2008; Henderson, 2010 for *Pteranodon* mass estimates), and we have little doubt that such predators could subdue these pterosaurs if they caught them (Fig. 4). Conversely, *Pteranodon* likely had a relatively low body density and their carcasses may have floated for sustained periods (Hone & Henderson, 2014). This would make them obvious targets for scavenging marine animals.

Evidence of the anacoracid shark *Squalicorax* consuming *Pteranodon* is known in the Niobrara (e.g. KU 972 - KU, Kansas University, USA; YPM 2597, YPM 42810 – Bennett, pers. comm. 06/16), and recent finds of Mooreville Chalk Formation *Pteranodon* also have bite marks attributed to *Squalicorax kaupi* (RMM 3274 and ALMNH 2014.1.200) (Ehret, Harrell & Ebersole 2015). This body of evidence, augmented with the *Cretoxyrhina-Pteranodon* association described here, and the recovery of fish remains within the gular region of *Pteranodon* specimens (Brown, 1943; Bennett, 2001) makes the trophic interactions of *Pteranodon* well understood compared to most other pterosaurs (Witton, 2018). However, such finds are still relatively rare occurrences - these seven associations are less than 1% of the >1100 specimens of *Pteranodon* on record. In contrast, at least ten palaeoecologically significant fossil associations are known for the Late Jurassic Solnhofen pterosaur *Rhamphorhynchus muensteri* (including five associations with the carnivorous fish *Aspidorhynchus acutirostris* (e.g. Frey &

Tishchlinger, 2012) and four examples of consumed items – see Witton, 2018 for a recent review). There are perhaps 150 specimens of *Rhamphorhynchus* in public collections, suggesting that recording of palaeoecological events is several times higher than in *Pteranodon* (>6%) despite a considerably smaller sample size. The taphonomic factors contributing to this difference may be worthy of further study.

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Figure captions.

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.

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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.

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.

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.

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.

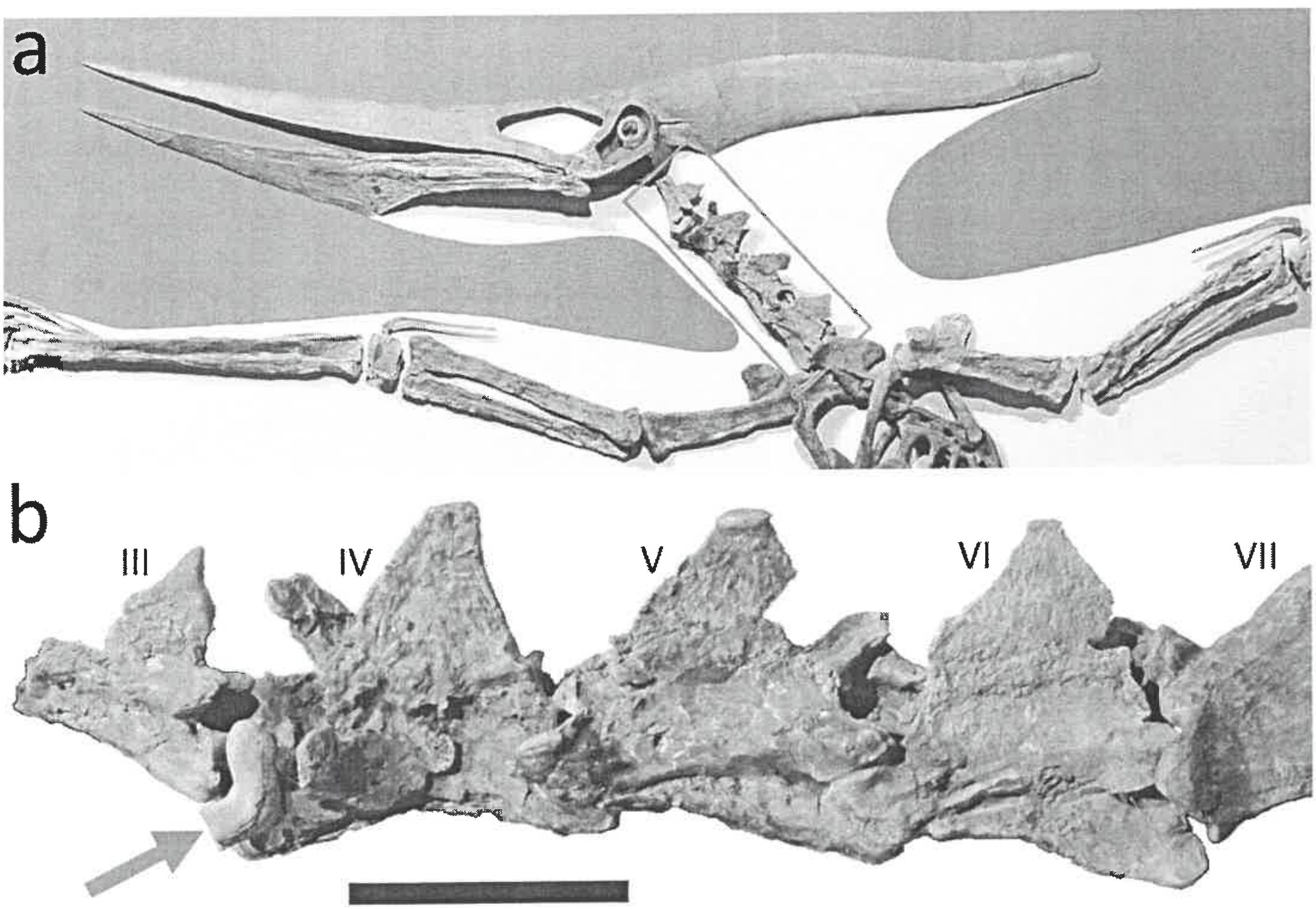

Figure 2

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.

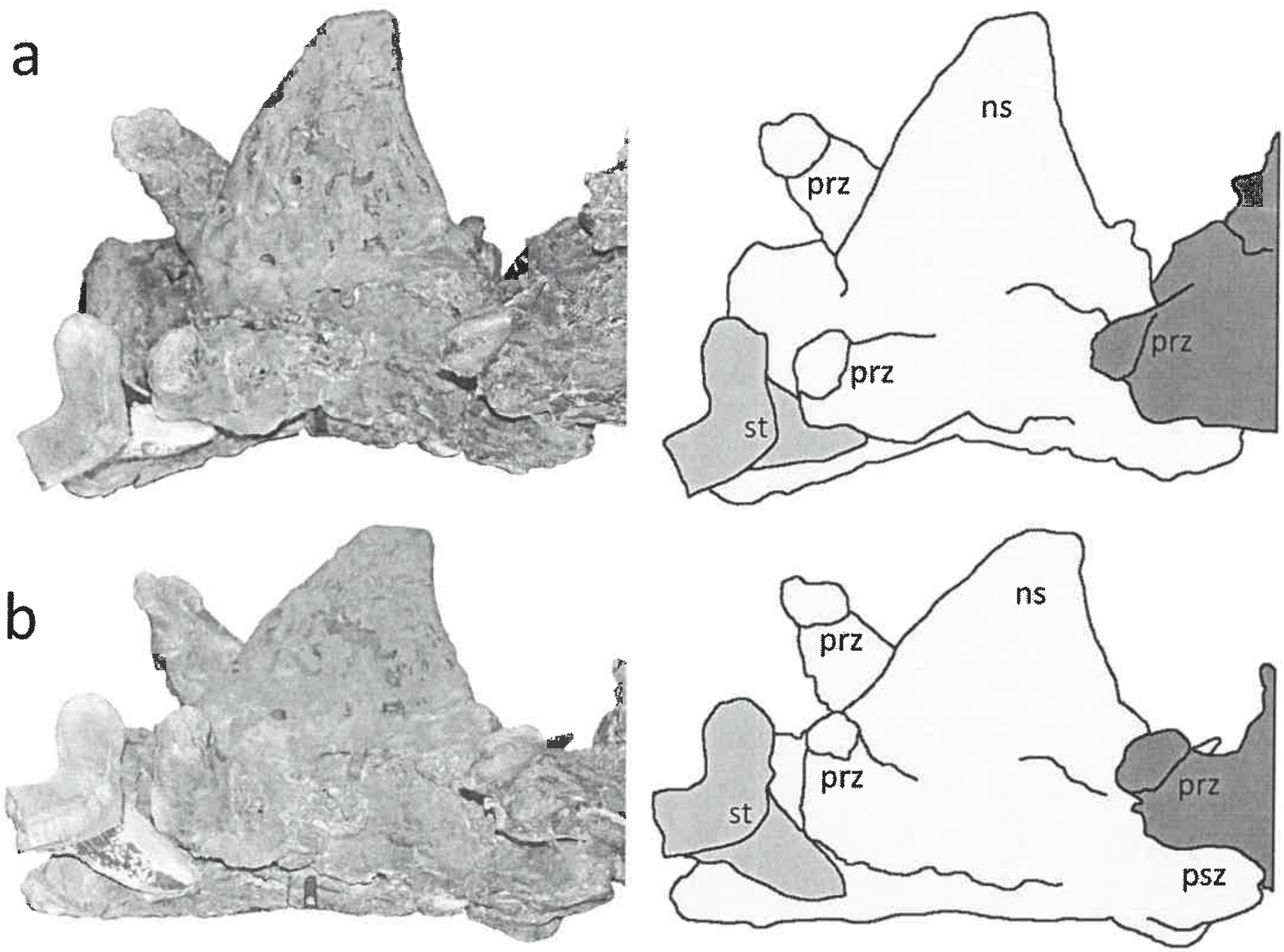

Figure 3

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.

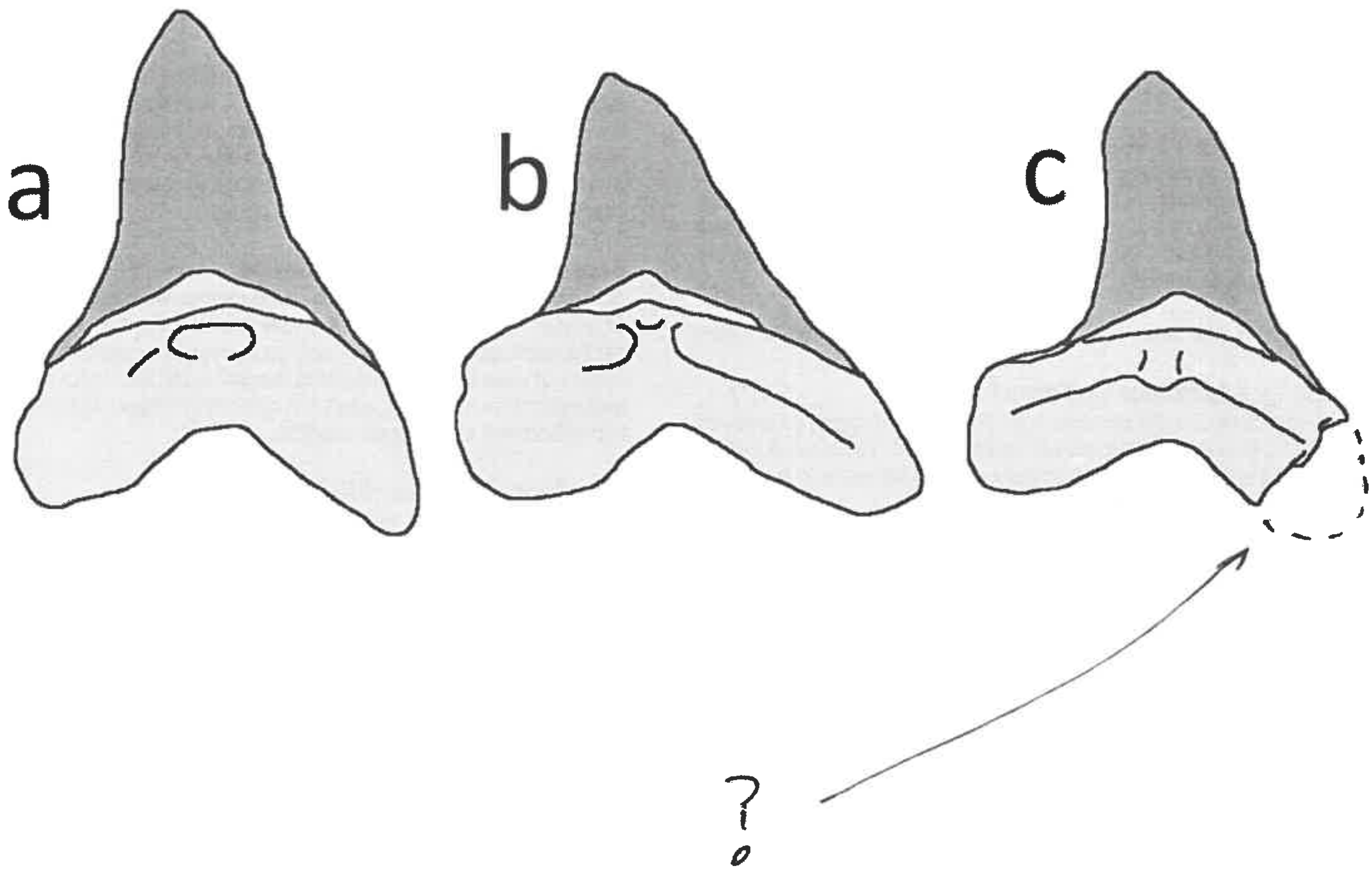

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Figure 4

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.