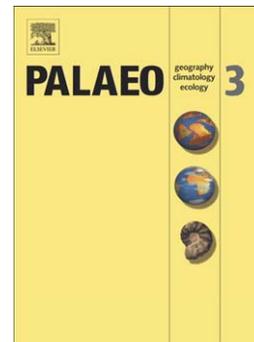# Accepted Manuscript

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New evidence for a trophic relationship between the dinosaurs *Velociraptor* and *Protoceratops*.

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Abstract

Reconstructing the palaeoecology of extinct tetrapods is fraught with difficulties.

Fossilized evidence of direct trophic interactions between tetrapods is rare, whether the interactions involve predation or scavenging. Typically this evidence is limited to preserved stomach contents or bite marks on bones (when they can be confidently attributed to specific taxa) that make it possible to begin to piece together the trophic webs that existed in ancient ecosystems. The dramatic 'fighting dinosaurs' fossil of a *Velociraptor* preserved in combat with a *Protoceratops* provides an outstanding, but still lone, example of the two taxa interacting. Here new evidence of a *Velociraptor* feeding on the carcass of a *Protoceratops* is presented, based on tooth-marked bones of the latter that were found in association with shed teeth of the former in Upper Cretaceous deposits at Bayan Mandahu, Inner Mongolia, China. In contrast to the case of the fighting dinosaurs, which seems to represent active predation by a *Velociraptor*, the tooth marks on the Bayan Mandahu material are inferred to have been produced during late-stage carcass consumption either during scavenging or following a group kill. Feeding by *Velociraptor* upon *Protoceratops* was probably a relatively common occurrence.

1. Introduction

Evidence of feeding by theropod dinosaurs is scarce in the fossil record (Carpenter, 2000; Farlow and Holtz, 2002; Hone and Rauhut, *in press*) and each new record adds significantly to our knowledge of theropod behaviour. In exceptional

cases both predator and apparent (or intended) prey can be positively identified based on an occurrence of associated remains of both animals (e.g. Buffetaut et al., 2004) or distinctive marks left on one by the other (e.g. see Erickson and Olson, 1996). Perhaps the most famous, and certainly the most dramatic, of these examples is the specimen known colloquially as the 'fighting dinosaurs', which was first reported by Kielan-Jaworowska and Barsbold (1972)..

This specimen preserves skeletons of the small dromaeosaurid *Velociraptor* and the small basal neoceratopsian *Protoceratops*, in a posture suggesting that the two individuals were locked in combat at the time of death and burial. The two animals appear to have perished simultaneously and it is possible that each caused the death of the other, although the exact circumstances surrounding their demise remain a focus of debate (Kielan-Jaworowska and Barsbold, 1972; Unwin et al. 1995; Carpenter, 2000). To date, the specimen continues to represent the only direct fossil evidence of interaction between these two taxa.

Here new information is presented supporting the inference that *Velociraptor* sometimes fed on *Protoceratops*, based on fragmentary remains of a basal neoceratopsian tentatively identified as *Protoceratops* from the Upper Cretaceous Wulansuhai Formation (Wei et al. 2005) of Bayan Mandahu, Inner Mongolia, China. These bones bear feeding traces attributable to a small dromaeosaur and were found in association with teeth that can be referred to *Velociraptor*.

2. Institutional abbreviations

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

IGM, Institute of Geology, Mongolian Academy of Sciences.

3. Locality and horizon

The fossil material described in this paper was collected from an aoelian sandstone exposure at the "Gate" locality (Eberth, 1993) at Bayan Mandahu, Inner Mongolia in August, 2008. Some further pieces were collected in June, 2009 following weathering at the site. Many of the specimens were found on the surface of a structureless red sandstone hillock situated within a shallow wash, whereas others were shallowly buried inside the hillock. The site lies within palaeogeographic zone 2 of Bayan Mandahu (Eberth, 1993), at the following coordinates: 41°44'18.1"N, 106°44'38.9"E. Bayan Mandahu beds (now attributed to the Wulansuhai Formation - Wei et al. 2005) are thought to be Campanian in age, and are considered laterally equivalent to the Djadokhta Formation of Mongolia (Jerzykiewicz et al. 1993).

4. Description

Over 60 pieces of bone and four teeth were collected at the site. All of the bone pieces are accessioned together as IVPP V16137, and include a large piece of lower jaw (dentary) and two detached teeth that were clearly derived from the maxilla or dentary of a basal neoceratopsian ornithischian dinosaur. Some of the bone fragments of IVPP V16137 bear bite marks. Associated with the neoceratopsian material were two teeth of a second dinosaur, a small dromaeosaurid theropod (IVPP V16138).

The neoceratopsian elements were found in a weathered and fragmented condition, with most pieces measuring just a few centimetres across. Individual pieces were found throughout the outcrop, suggesting that they may represent a variety of anatomical regions. Much of the skeleton had clearly been destroyed through erosion, and some of the remaining fragments were not recoverable due to their poor condition. However, it is possible that the specimen was largely complete and even articulated when first exposed. The partial jaw and preserved teeth (Fig 1A) strongly resemble those of *Protoceratops* (You and Dodson, 2004), which is by far the most common dinosaur in the formation (Jerzykiewicz et al., 1993 and personal observations). Some basal neoceratopsian specimens collected at Bayan Mandahu have been identified as *Bagaceratops* and *Udanoceratops*, and a partial skull from this locality was the basis for the new genus *Magnirostris* (Dong and Currie, 1993; Alifanov, 2008). However, none of these taxa is thought to approach the abundance of *Protoceratops*, and *Udanoceratops* is also much larger, with a skull length of up to one metre. Furthermore, the lone specimen assigned to *Magnirostris* is likely to pertain to *Bagaceratops* (Makovicky and Norell, 2006). IVPP V16137 could therefore conceivably represent a specimen of *Bagaceratops*, or a young juvenile *Udanoceratops*, but the balance of probability favours identification as *Protoceratops*. We refer to this specimen as *Protoceratops* for the remainder of this paper, while conceding that it might represent a different, but very closely related, basal neoceratopsian taxon.

The two small theropod teeth (IVPP V16138) were recovered from just beneath

the sediment surface at approximately the central point of the oval distribution of the

Protoceratops remains (Fig. 1B). The teeth can be identified as those of a

velociraptorine dromaeosaur sensu Lindgren et al. (2008), based on the elongate shape

and large size of the posterior denticles in comparison to the greatly reduced denticles

on the anterior carina (Currie et al., 1990). The only velociraptorine whose presence

has been recorded at Bayan Mandahu is *Velociraptor* itself, which is known from

several partial juvenile skeletons as well as other finds of isolated teeth (Jerzykiewicz

et al., 1993), and we provisionally assign IVPP V16138 to this taxon. The Djadokhta

Formation dromaeosaur genus *Tsaagan* (Norell et al., 2006), known from a single

specimen, is the only other Campanian velociraptorine known from Asia. It is unlikely

that isolated teeth of *Tsaagan* and *Velociraptor* can be reliably distinguished from

each other, so there is a possibility that IVPP V16138 represents *Tsaagan* or even an

undescribed velociraptorine. However, we regard assignment to *Velociraptor* as most

probable, based on the documented occurrence of this taxon at Bayan Mandahu from

several specimens.

The *Velociraptor* teeth are small, recurved and serrated. As in other

velociraptorines, the posterior denticles are much more elongate mesiodistally than

the anterior ones (Currie et al., 1990). The larger tooth shows extensive wear and is

blunt at the tip, a pattern more consistent with abrasion damage incurred during

normal feeding than with weathering. The apical part of the second tooth is broken

away. The break may have occurred due to erosion following exposure of the

specimen, but this seems unlikely given the otherwise excellent quality of the tooth

and the nature of the weathering damage on the *Protoceratops* bones and teeth. The

more complete, heavily worn tooth is the larger and more rounded of the two, and

probably represents a premaxillary tooth. It was presumably an old tooth that was

close to being shed. The apically broken tooth is smaller and thinner, and probably

from the maxilla or the posterior part of the dentary (based on Currie et al., 1990 and

Norell et al., 2006).

4.1 Feeding traces

Theropod tooth marks on bone often consist of either multiple subparallel grooves

made by several adjacent teeth in the dental arcade (as from the teeth of the

premaxilla; Hunt et al., 1994), or single scores where an errant tooth has contacted the

bone (Currie and Jacobsen, 1995). Marks of both kinds presumably result from

scraping movements in which the teeth are drawn over the carcass to remove flesh for

consumption.

Among the recovered fragments of *Protoceratops* are at least eight pieces that

each exhibit at least one, and more typically several, marks interpreted as feeding

traces (Fig. 2). These are typically shallow subparallel grooves that run across the

cortex of the bone. Such grooves do not exceed a depth of one millimetre, and do not

penetrate the cortex. By contrast, two pieces exhibit semi-circular 'bite and drag'

marks (Fig. 2B, C), implying the teeth were driven deep into the bony cortex and then

dragged through it (equivalent to the 'puncture and pull' marks of Erickson and Olson

(1996)). One piece of bone bears bite marks on both sides, but in all other cases the

marks are restricted to one side alone (although most of the pieces represent one-sided cortical fragments rather than preserving the entire thickness of a bone).

The distribution of the tooth marks on the elements described here matches patterns seen in other bones showing damage that can be attributed to theropod bite traces (Hunt et al., 1994; Jacobsen, 1998). These records are interpreted as accidental marks made during feeding, as opposed to deliberate bone biting (Jacobsen, 1998). Notably, one documented example of bite marks has been positively attributed to a velociraptorine: in a case described by Currie and Jacobsen (1995), a *Saurornitholestes* marked a bone of an azhdarchoid pterosaur during a presumed episode of scavenging, even leaving a broken tooth embedded in the bone in addition to the marks on the surface.

Weathering of the cortical surface can be ruled out as the cause of the marks on IVPP V16137. Several of the marked elements were discovered in situ, and in two others the bone surface showing the bite marks was face down on the sediment when the specimen was found. Bones at Bayan Mandahu are a pale yellow colour when first exposed (DWEH pers. obs.), but tend to lighten in colour after lying on the surface for any length of time and ultimately become white. Many of the tooth-marked pieces of IVPP V16137 were still yellow when recovered from below the surface, ruling out erosion and later reburial. Other pieces of bone from the surface do exhibit weathering, which tends to leave a diagnostic pattern on the bone surface (see Fig. 2D). Other taphonomic effects such as distortion, chemical wear or reworking are unlikely to have had a significant impact on the material, given the generally high quality of the

bone surfaces. Apart from fragmentation, the individual pieces of bone have suffered little damage apart from the feeding traces themselves.

5. Discussion

The specimens described in this paper provide important independent confirmation of a previously suggested pattern of trophic interaction between two dinosaurian taxa, namely feeding by *Velociraptor* (IVPP V16138) upon *Protoceratops* (IVPP V16137). Even if one or both of these specimens has been misidentified at the generic level, they clearly still support a more general trophic relationship between velociraptorine dromaeosaurids and basal neoceratopsians in the Late Cretaceous of Asia. However, the "fighting dinosaurs" specimen from the Upper Cretaceous Djadokhta Formation of the Tögrögiin Shiree locality, Mongolia (Kielan-Jaworowska and Barsbold, 1972) remains the only direct evidence that *Velociraptor* actively preyed on *Protoceratops*. In this specimen the raptorial pedal claw of a *Velociraptor* is lodged in the throat region of a *Protoceratops*, suggesting that the former combatant killed the latter. However, the right arm of the *Velociraptor* is also locked firmly between the jaws of the *Protoceratops*, and it is possible that this enigmatic specimen represents not a predator/prey interaction but rather a chance encounter between the two animals that escalated into combat. In the case of IVPP V16137 and IVPP V16138, it cannot be definitively determined whether the *Velociraptor* was feeding on a *Protoceratops* it had killed or simply scavenging on an individual that had died previously.

However, the Bayan Mandahu material does reinforce the inference from the fighting dinosaurs that *Protoceratops* was a part of the diet of *Velociraptor*, whether as prey or as carrion. The fighting dinosaurs specimen can no longer be considered to record a unique example of trophic interaction between these taxa, and indeed such interactions may have been common given the prevalence of *Protoceratops* and *Velociraptor* in Djadokhta-equivalent sediments. Velociraptorine teeth have been reported in association with unspecified herbivorous dinosaurs at Bayan Mandahu (Jerzykiewicz et al., 1993), and in most cases the taxa involved were presumably *Velociraptor* and *Protoceratops*. Further possible examples of this association have been observed in the field at Bayan Mandahu by the present authors. However, actual bone damage resulting from feeding traces has not been previously reported from this locality.

Velociraptorine teeth were clearly vulnerable to breakage during feeding, even upon a carcass that lacked particularly robust bones (Currie and Jacobsen, 1995). Shedding of teeth during feeding was probably a common event for theropods (Hone and Rauhut, *in press*), which may explain the regular association of velociraptorine teeth with other dinosaur fossils at Bayan Mandahu. In any event, the prevalence of theropod tooth loss during feeding lends support to the idea that the velociraptorine teeth described in this paper (IVPP V16138) belonged to an individual that actually inflicted the damage seen on the bone fragments of IVPP V16137, rather than simply being associated with the bone fragments by a vagary of preservation.

A few tentative inferences about the mode of feeding in this case are possible.

The sequence of consumption of various fleshy carcass elements by modern mammalian carnivores is remarkably consistent, although patterns of bone consumption display more variation (Blumenschine, 1987). The lightly-built skull and thin, recurved teeth of *Velociraptor* do not show any obvious adaptations to osteophagy and are small in absolute terms compared to the bones of a *Protoceratops*. Quadrupedal ornithischians can reasonably be assumed to have been broadly similar to extant ungulates in the volumetric distribution of their musculature. We therefore infer that a velociraptorine feeding upon a ceratopsian might have proceeded in essentially the same sequence seen in modern, non-osteophagous mammalian carnivores, with initial consumption of bowel and hindquarter flesh, followed by forequarter flesh, and finally head and neck flesh (Blumenschine, 1987). Thus, we consider the presence of bite marks on the *Protoceratops* jaw from Bayan Mandahu to represent late-stage carcass consumption by *Velociraptor*. This interpretation is further supported by the fact that the bite marks are numerous, suggesting repeated bites close to the cortical surface of the bone. This would probably not have occurred unless the majority of the available muscle mass had already been stripped off and the dromaeosaur was feeding close to the bone. The broken tooth also suggests an instance of significant, although not necessarily very forceful, tooth-bone contact. This would seem unlikely for an animal during normal feeding and is reminiscent of the case of tooth breakage that was previously inferred by Currie and Jacobsen (1995) to have taken place during a scavenging event by a velociraptorine.

The sizes of the two animals presented here provide a basis for further inferences.

The broader and more complete tooth of IVPP V16138 is comparable in size to the largest tooth preserved in the left maxilla of the fighting *Velociraptor* (IGM 100/25), which has a skull length of about 240 mm (Norell et al., 2006: Fig. 6b). The total body length of the fighting *Velociraptor* is approximately 1.7 m (Carpenter, 2000), whereas Turner et al. (2007: supplemental information) estimated the length and mass of an adult specimen of *Velociraptor* as 1.5 m and 24 kg respectively. Accordingly, IVPP V16138 and the fighting *Velociraptor* were almost certainly both adults, and were of broadly comparable size. The larger tooth of the *Protoceratops* IVPP V16137 has a preserved mesiodistal width of 12.2 mm, and this figure appears to be up to 25% smaller than the true value as a result of damage to one side (either mesial or distal) of the tooth (i.e. the tooth may have been over 16 mm wide). Accordingly IVPP V16137 also represents an adult individual. To our knowledge, the only published mass estimates of *Protoceratops* are the very divergent ones by Colbert (1962) and Seebacher (2001). Colbert suggested a mass of 177 kg, probably based on an adult specimen with a body length of approximately 2 m (Dodson, 1996), while Seebacher calculated 23.7 kg based on an assumed length of 1.4 m. Given the discrepancy between these figures, a careful reanalysis of the probable mass of *Protoceratops* would be valuable.

However, even assuming that Seebacher (2001) was correct in suggesting that *Protoceratops* had a relatively low mass in proportion to its length, it seems unlikely that a single adult *Velociraptor* (i.e. IVPP V16138) could have consumed almost all of the flesh on an adult *Protoceratops* (i.e. IVPP V16137) during a single bout of feeding.

Group hunting has been suggested for dromaeosaurs in the past (Ostrom, 1990 - though not *Velociraptor* explicitly) so there is also the possibility that a group was feeding on the carcass. Accordingly, the inference of late stage feeding in the mandibular region further implies either that at least one individual *Velociraptor* was scavenging upon a carcass that had already been partly defleshed, or that several individuals of *Velociraptor* killed the *Protoceratops* and consumed so much of the readily accessible flesh of the limbs and torso that they proceeded to attack the head. The two possibilities are impossible to distinguish with certainty, although the occurrence of only two shed crowns may suggest that IVPP V16138 is more likely to represent a single scavenging individual than the sole evidence of a predatory group (tooth crowns are very common at inferred dromaeosaur kill sites – see Ostrom, 1990; Roach and Brinkman, 2007). Furthermore, it is possible that even a carcass as small as about 25 kg (including bones and other inedible tissues) would have provided a significant meal for an entire pack of small dromaeosaurs. Scavenging is more likely than predation to involve late-stage feeding, since scavengers often encounter carcasses that have already been partly denuded of flesh.

The inference of either scavenging or group predation contrasts with the 'fighting dinosaurs', which have traditionally and understandably been interpreted as a predation attempt by a single attacker (Kielan-Jaworowska and Barsbold, 1972; Ostrom, 1990; Carpenter, 2000). The fighting *Protoceratops* was a relatively small individual with a body length of approximately 1.3 m, falling well short of the typical adult length of approximately 2 m (estimated from You and Dodson, 2004: Figure

22C). The individual may have been a juvenile, a possibility consistent with the

hypothesis that theropods preyed primarily upon juveniles (Hone and Rauhut, *in*

press).

In summary, the fighting dinosaurs represent an apparent case of predation by an

adult *Velociraptor* upon a small and possibly juvenile *Protoceratops*, but taken in

isolation this famous specimen cannot indicate whether such active predation was a

common or a rare event. The new specimens from Bayan Mandahu described in this

paper strongly suggest that an adult *Protoceratops* acted as a food source for either a

group of predatory *Velociraptor* or, more likely, a scavenging individual. Taken

together, the two cases suggest that feeding by *Velociraptor* on *Protoceratops*, in the

context of either scavenging or predation, was a relatively common occurrence. This

is hardly a surprising conclusion, considering the abundance of *Protoceratops* and

Velociraptor in Djadokhta-equivalent beds in both Inner Mongolia and Mongolia

proper. *Protoceratops* is by far the most common dinosaur in such deposits, and

Velociraptor probably the most common theropod. However, the value of positive

evidence for such a trophic relationship should not be underestimated, given that

studies of dromaeosaurid ecology and hunting style (Ostrom, 1990; Fastovsky and

Smith, 2004; Roach and Brinkman, 2007) necessarily draw inferences from a very

limited body of primary data.

Acknowledgements

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Figure Captions:

Fig. 1 A. Teeth of *Protoceratops* IVPP V16137 and B. Teeth of *Velociraptor* IVPP
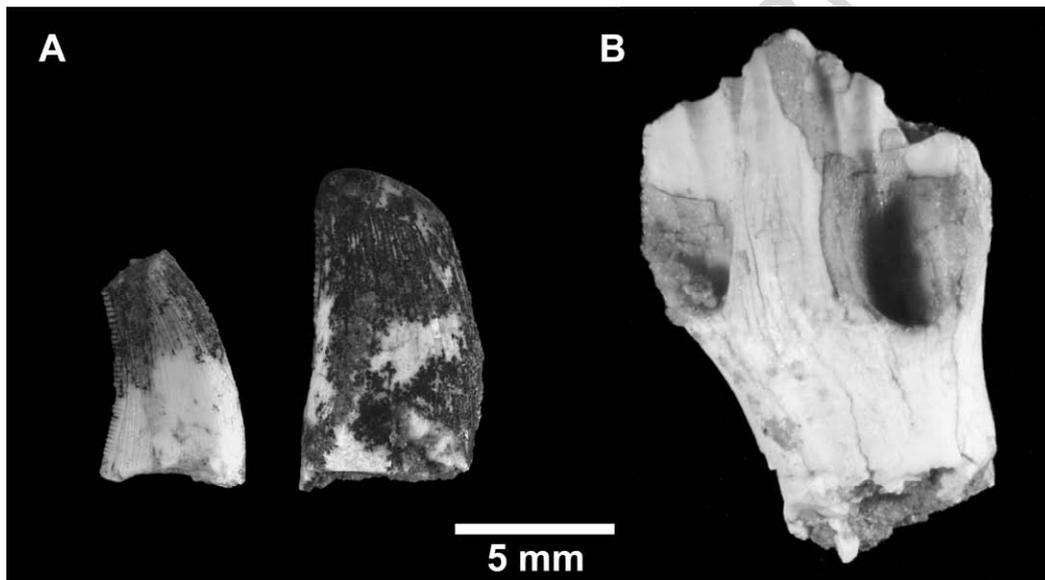
V16138 (Scale bar for each is 5 mm).

Fig. 2 A. Bite marks as faint drags on the surface of the bone as indicated by the white arrows (scale bar 5 mm).B. Faint (white arrows) and deeper, curved bite and drag marks (black arrows) (scale bar 2.5 mm).C. A single curved deep mark (white arrow) (scale bar 5 mm). D. Piece of eroded *Protoceratops* bone showing the characteristic pattern resulting from natural wear, which does not resemble the bite marks seen in A–C (scale bar 5 mm).