A tyrannosaur jaw bitten by a confamilial: scavenging or fatal agonism?

PHIL R. BELL AND PHILIP J. CURRIE

LETHAIA

A partial dentary of an adult tyrannosaur from the Dinosaur Park Formation of Alberta, Canada, preserves the embedded tooth of another tyrannosaur within the bone. The specimen's incompleteness precludes generic identification of either the jaw or the embedded tooth, although *Gorgosaurus* and/or *Daspletosaurus* are most likely given the stratigraphic position. The absence of healing around the lesion indicates the bite took place either post-mortem or within weeks prior to the death of this animal. A post-mortem bite can be explained by confamilial or cannibalistic scavenging. Alternatively, the bite would represent a perimortem instance of intrafamilial aggression that may have resulted in the death of that animal. An estimated 6053N of bite force was required to produce the bite mark. This specimen provides the best evidence for aggressive peri- or post-mortem confamilial interaction among tyrannosaurs and corroborates previous studies based on inferred tooth marks. □ *Alberta, behaviour, Campanian, Cretaceous, Dinosaur Park Formation, Theropoda, Tyrannosauridae.*

Phil R. Bell [pbell@ualberta.ca] and Philip J. Currie [philip.currie@ualberta.ca], Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada; manuscript received on 27/4/2009; manuscript accepted on 24/6/2009.

Although tooth-marked bone is relatively common in the fossil record (Fiorillo 1991), specific identification of the trace is often difficult. Previously, identification of inter- and intraspecific interactions from tooth-on-bone trauma involving dinosaurs has relied on tooth spacing (Jacobsen 1997, 1998; Chure *et al.* 2000; Rogers *et al.* 2003), denticle scours (Jacobsen 1997, 2001; Rogers *et al.* 2003) and latex casts of tooth-impressions in bone (Erickson & Olson 1996).

Currie & Jacobsen (1995) described the first instance of tooth-marked bone with an associated tooth still embedded in the bone. The described specimen is an azhdarchid pterosaur tibia (TMP 92.83.2) from the Dinosaur Park Formation of Alberta. The specimen preserves three transverse tooth marks and a fourth wound with the embedded tip of a tooth from the small theropod, *Saurornitholestes langstoni*. The large size of the target animal compared with its assailant and the absence of healing around the bite marks led these authors to conclude that the theropod was probably scavenging on the carcass of the pterosaur. A similar example involving an azhdarchid cervical vertebra and the embedded tooth of a spinosaurid provides evidence that spinosaurs had broader diet than previously suspected (Buffetaut *et al.* 2004). A third specimen consisting of a *Hypacrosaurus stebingeri* fibula (MOR 549) preserves the embedded tooth of a tyrannosaurid (Currie & Jacobsen 1995; Farlow & Holtz 2002). The absence of remodelled bone (healing) around the lesions in all of the aforementioned specimens indicates that the bites took place post-mortem or during attacks that led to the deaths of these individuals.

A partial left dentary (TMP 1996.05.13) from an adult tyrannosaurid preserves the broken tooth of an attacker embedded within the bone. This specimen, mentioned but not described by Tanke & Currie (2000), represents the first occurrence of a theropod bone with an embedded tooth. Evidence for intraspecific and intrafamilial antagonistic behaviour in large theropods has been previously described from bite marks on bones (Petersen *et al.* 1972; Tanke & Currie 1995, 2000) and teeth (Tanke & Currie 1995, 2000; Tanke & Rothschild 1997). The embedded tooth in TMP 1996.05.13 provides unequivocal evidence for intrafamilial (if not intraspecific) interaction between tyrannosaurs and offers insights into the behaviour of this group.

Institutional abbreviations – MOR, Museum of the Rockies, Bozeman, Montana; RSM, Royal Saskatchewan Museum Fossil Research Station, Eastend, Saskatchewan; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta.

Geology and locality

TMP 1996.05.13 was collected from the 'Steveville pocket' of Dinosaur Provincial Park near the ghost town of Steveville in southern Alberta, Canada. The

specimen was found as an isolated element within channel sandstones of the Dinosaur Park Formation that were laid down ~76.5–74.8 Ma on a broad alluvial plain west of the Bearpaw Sea (Eberth & Deino 1992; Eberth 2005). Two tyrannosaurids are known from this stratigraphic interval; *Gorgosaurus libratus* and the comparatively rare *Daspletosaurus* sp. (Currie 2005).

Description

TMP 1996.05.13 comprises the distal portion of a large, tyrannosaur dentary including the symphysis, alveoli d1–7 and part of alveolus d8 (Figure 1). Germ tooth VI is the only tooth still *in situ*. The maximum depth of the dentary is 105 mm. When 71 dentaries of tyrannosaurids (*Albertosaurus*, *Daspletosaurus*, *Dilong*, *Gorgosaurus*, *Tarbosaurus* and *Tyrannosaurus*) are compared with femora, bivariate analysis of the logarithms of dentary depth (at the front) to femur length produce the equation $y = 1.3528x - 1.9953$ ($r^2 = 0.9527$). This suggests that the femur length of

TMP 1996.05.13 would have been approximately 930 mm long. Using the equation $y = 1.0276x + 0.8437$ (Currie 2000, 2003) to compare logarithms of femoral lengths (x) with body lengths (y) in a variety of theropods, the body length of TMP 1996.05.13 can be estimated as 7 m. Symphyseal length/symphyseal depth is 0.97, placing it within the *Daspletosaurus-Gorgosaurus* zone (Therrien *et al.* 2005). 'Wrinkling' of the tooth enamel, which is variably present in *Daspletosaurus*, is absent, preventing differentiation between those two taxa, which co-occur in the Dinosaur Park Formation (Currie 2005).

The broken tip of a tyrannosaur tooth is embedded in the ventrolateral surface of the dentary at about the base of the intermandibular symphysis (Fig. 1B). The tooth consists of the apical 6 mm and measures 6.5 mm anteroposteriorly and 5 mm labiolingually. Because the tooth is fragmentary, it was not possible to determine the absolute size of the animal to which it belonged. Carinae are present on the anterior and posterior edges of the tooth suggesting that it came from either the dentary or maxillary (rather than the premaxillary) tooth row. As embedded, the carinae
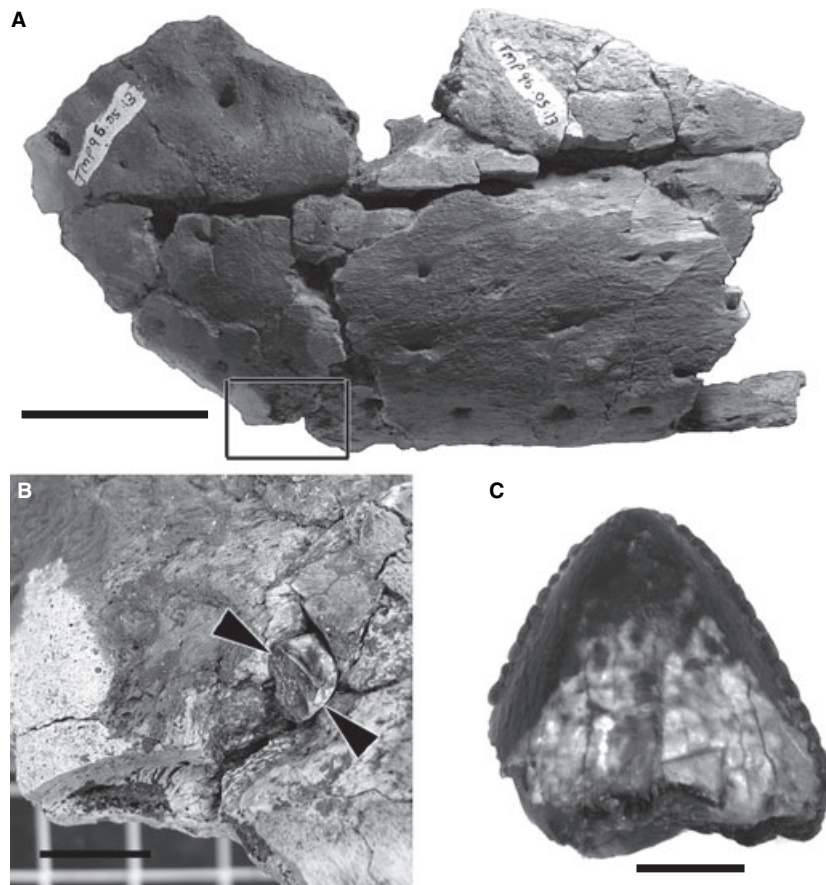

Fig. 1. The symphyseal region of a tyrannosaur left dentary (TMP 1996.05.13). A, lateral view; B, close up of the region outlined by the box in A from a ventral view, showing the location of the embedded tooth (arrow); C, tyrannosaur tooth found embedded in TMP 1996.05.13. Scale bar: A = 5 cm, B = 1 cm, C = 2 mm.

are aligned labiolingually to the dentary. The sheared base of the tooth lies flush with the surface of the dentary and there is no sign perilesional reactive bone growth. The bone immediately surrounding the tooth is damaged, but it is unknown whether this occurred at the time of injury or at some other post mortem stage. A typical tyrannosaurid denticle ratio of two per mm (Currie *et al.* 1990) is apparent when the tooth is removed from the lesion (Fig. 1C). Both the size and shape of the denticles identify the tooth as that of a large, adult tyrannosaurid (Currie *et al.* 1990).

Discussion and conclusions

TMP 1996.05.13 is identified as an adult tyrannosaurid. It is not possible to determine whether it is *Daspletosaurus* or *Gorgosaurus* because of the fragmentary nature of the specimen; however, it is tenable that one or both elements belong to *G. libratus* given the relative abundance of that taxon in the Dinosaur Park Formation (Currie 2005). Based on the location and labiolingual alignment of the carinae of the broken tooth, the tooth was emplaced during a dorsoventrally directed bite approximately perpendicular to the long axis of the dentary.

Using the equation, $y = 2303.402x + 646.634$ (Erickson *et al.* 1996) to determine the bite force in Newtons (y) required to penetrate cortical bone of thickness $x,$ we estimate that 14 479 N of force would be required to produce an equivalent bite mark for *Tyrannosaurus rex.* However, because this equation is based on tooth measurements obtained for *T. rex* and because *T. rex* has more massive teeth compared with either *Daspletosaurus* or *Gorgosaurus* (including the embedded tooth in TMP 1996.05.13), we multiplied the *T. rex* force by the ratio of the surface areas of the embedded tooth and the apical 6 mm of an equivalent *T. rex* maxillary tooth (RSM P2523.8) (Force of tooth penetration is proportional to its surface area in contact with surrounding bone; Erickson *et al.* 1996). This yielded a conservative estimate of 6053 N required to embed the tooth in TMP 1996.05.13, at which point it broke. This value is similar to lower estimates of bite force (6410 N) calculated from a *T. rex* bite on a *Triceratops* ilium (Erickson *et al.* 1996), which had a thinner cortex (2.5 mm) than the dentary cortex of TMP 1996.05.13 (>6 mm) perforated by the embedded tooth.

Although fractures (including penetrating injuries) begin to heal almost immediately, the osseous response to trauma (i.e. remodelling and callus formation) is not apparent until the third to ninth week (Lovell 1997). The lack of bone remodelling around the embedded tooth in TMP 1996.05.13 indicates the victim died almost immediately or within weeks of the attack. Alternatively, TMP 1996.05.13 was already dead and being fed upon (scavenged) when the tooth was emplaced. As TMP 1996.05.13 was an isolated specimen, we are unfortunately unable to test either hypothesis. Although previously documented cases of teeth embedded in bone record feeding behaviour, TMP 1996.05.13 is intriguing as it also documents intrafamilial behaviour. The term 'intrafamilial' is used here in preference to intraspecific as neither the dentary nor the embedded tooth are identifiable to the level of genus or species.

Tanke & Currie (2000) described multiple instances of face-biting behaviour in large theropods from healed and unhealed cranial lesions. They categorized these lesions into several types, namely: punctures, scores or tooth drags, serration marks and embedded and broken teeth; however, only the latter two categories permit positive identification of the offending animal (Jacobsen 1998), neither of which have been observed on the skulls of tyrannosaurs, except TMP 1996.05.13. TMP 1996.05.13 therefore provides the first unequivocal evidence for face-biting behaviour among members of the Tyrannosauridae and supports the conclusions of Tanke & Currie (2000).

Traumatic cranial lesions in tyrannosaurs and other large theropods attributed to intra- and interspecific face-biting behaviour may have been incurred for several reasons, including establishment of pack dominance, courtship/mating, territoriality or even play (Tanke & Currie 2000). Regarding TMP 1996.05.13, only play can be ruled out with any certainty as this behaviour is typically restricted to juveniles of modern terrestrial predators (Schaller 1972). The bite described here was probably not fatal in itself but may have incapacitated the animal and/or enabled other bites to do the killing (Schaller 1972). A second possibility is that TMP 1996.05.13 died of unrelated causes within days or weeks of the attack that left the tooth imbedded in its dentary. In the absence of other skeletal evidence, it is impossible to determine the fate of the animal. Fatal intraspecific encounters are well documented in extant crown group archosaurs – crocodiles and birds (Clevenger & Roest 1974; Fisher 1975; Cawston 1983; Rendell 1993; Webb & Manolis 1998; Andersen 2004) – and are usually attributed to territoriality and dominance displays.

If the bite took place after the death of TMP 1996.05.13, then feeding behaviour, and possibly cannibalism, is (are) implied. However, neither the dentary nor the embedded tooth tip of TMP 1996.05.13 can be identified to species level, and therefore cannot be used to demonstrate cannibalism. Although cannibalism has been suggested in tyrannosaurids (Jacobsen 1998), this behaviour has only been conclusively

documented amongst theropods in the abelisaurid, *Majungasaurus crenatissimus* (Rogers *et al.* 2003). Putative cannibalism in *Coelophysis bauri* (Colbert 1947, 1995) has been shown to be a case of erroneous interpretation and misidentification (Gay 2002; Nesbitt *et al.* 2006). Rare examples of tooth-marked tyrannosaur bones from the Dinosaur Park Formation suggest that tyrannosaurs did occasionally feed on the carcasses of confamilials (Jacobsen 1998).

Presently, TMP 1996.05.13 provides the most reliable evidence for confamilial face-biting among tyrannosaurs although it cannot be demonstrated whether this instance reflects peri- or post-mortem behaviour. Using the same criteria used by Rogers *et al.* (2003) for *M. crenatissimus*, intraspecific interaction can best be identified where unequivocal tyrannosaur bite marks/feeding traces (e.g. embedded teeth, serration marks) are found on the bones of another tyrannosaur from a formation where only one species of tyrannosaur is known. Further field work in the Horseshoe Canyon, Frenchman, Willow Creek and Scollard Formations of western Canada – where only a single tyrannosaur species is known (*Albertosaurus sarcophagus* is the only tyrannosaurid present in the Horseshoe Canyon Formation; *Tyrannosaurus rex* is the sole representative in the latter three) – may provide the best chances of identifying intraspecific agonistic or cannibalistic behaviour among tyrannosaurs.

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