

Physical evidence of predatory behavior in *Tyrannosaurus rex*

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Feeding strategies of the large theropod, *Tyrannosaurus rex*, either as a predator or a scavenger, have been a topic of debate previously compromised by lack of definitive physical evidence. Tooth drag and bone puncture marks have been documented on suggested prey items, but are often difficult to attribute to a specific theropod. Further, postmortem damage cannot be distinguished from intravital occurrences, unless evidence of healing is present. Here we report definitive evidence of predation by *T. rex*: a tooth crown embedded in a hadrosaurid caudal centrum, surrounded by healed bone growth. This indicates that the prey escaped and lived for some time after the injury, providing direct evidence of predatory behavior by *T. rex*. The two traumatically fused hadrosaur vertebrae partially enclosing a *T. rex* tooth were discovered in the Hell Creek Formation of South Dakota.

One of the most daunting tasks of paleontology is inferring the behavior and feeding habits of extinct organisms. Accurate reconstruction of the lifestyle of extinct animals is dependent on the fossil evidence and its interpretation is most confidently predicated on analogy with modern counterparts (1–6). This challenge to understanding the lifestyle of extinct animals is exemplified by the controversy over the feeding behavior of the Late Cretaceous theropod *Tyrannosaurus rex* (3, 7–17). Although predation and scavenging have often been suggested as distinct feeding behavior alternatives (3, 7–9, 11–17), these terms merit semantic clarification. In this study, predation is considered a subset of feeding behavior, by which any species kills what it eats. Although the term “predator” is used to distinguish such animals from obligate scavengers, it does not imply that the animal did not also scavenge.

Ancient diets can be readily reconstructed on the basis of the available evidence, although their derivation (e.g., predation or scavenging behavior) often remains elusive. Speculation as to dinosaur predation has ranged from inferences based on skeletal morphology, ichnofossils such as bite marks, coprolites, stomach contents, and trackways and, by more rarely, direct predator–prey skeletal associations (3, 4, 18–23).

Direct evidence of predation in nonavian dinosaurs other than tyrannosaurids has been observed in rare instances, such as the *Deinonychus*–*Tenontosaurus* kill site of the Cloverly Formation where the remains of both were found in close association along with shed teeth (9, 24), and the “fighting dinosaurs” from the Gobi Desert, in which a *Velociraptor* and *Protoceratops* were found locked in mortal combat (9, 17). The evidence on tyrannosaurids is more limited. Putative stomach contents, such as partially digested juvenile hadrosaur bones, have been reported in association with tyrannosaurid remains (3, 12, 18). This latter instance only represents physical evidence of the last items consumed before the animal’s death, an indicator of diet but not behavior.

Mass death assemblages of ornithischians frequently preserve shed theropod teeth (6, 22, 24). Lockley et al. (23) suggest such shed teeth are evidence of scavenging behavior. It is widely argued that *T. rex* procured food through obligate scavenging rather than hunting (11, 14, 25–27) despite the fact that there is currently no modern analog for such a large bodied obligate

scavenger (26). Horner (25) argued that *T. rex* was too slow to pursue and capture prey items (14) and that large theropods procured food solely through scavenging, rather than hunting (11, 25). Horner also suggested that the enlarged olfactory lobes in *T. rex* were characteristic of scavengers (25). More recent studies (28, 29) determined the olfactory lobes of modern birds are “poorly developed,” inferring that enlarged olfactory lobes in *T. rex* are actually a secondary adaptation for predation navigation “to track mobile, dispersed prey” (30). *T. rex* has a calculated bite force stronger than that of any other terrestrial predator (7), between 35,000 and 57,000 Newtons (30, 31), and possible ambulatory speeds between 20 and 40 kph (7, 15, 16), documenting that it had the capability to pursue and kill prey items.

Healed injuries on potential prey animals provide the most unequivocal evidence of survival of a traumatic event (e.g., predation attempt) (3, 32, 33), and several reports attribute such damage to *T. rex* (4, 17, 19, 20). These include broken and healed proximal caudal vertebral dorsal spines in *Edmontosaurus* (17) and healed cranial lesions in *Triceratops* (4, 19). Although the presence of healed injuries demonstrates that an animal lived long enough after the attack to create new bone at the site of the damage (a rare occurrence in the fossil record) (19), the healing usually obliterates any clear signature linking the injury to a specific predator. Bite traces (e.g., raking tooth marks on bone and puncture wounds in the bones of possible prey animals) attributed to *T. rex* (2, 4, 19) are ambiguous, because the damage inflicted upon an animal during and after a successful hunt mirrors feeding during scavenging. This makes distinction between the two modes of food acquisition virtually impossible with such evidence (3, 34–38).

Tooth marks, reported from dinosaur bone-bearing strata worldwide (e.g., 2–4, 8, 19, 20, 39, 40), are further direct evidence of theropod feeding behavior, attributed by some to specific theropod groups (2, 4, 19, 20). Happ (19) and Carpenter (17) identified theropods to family and genus by matching spaces to parallel marks (traces) with intertooth distance. Happ (19) described opposing conical depressions on a left supraorbital *Triceratops* horn that was missing its distal third (tip), attributing them to a bite by either a *T. rex* or a crocodylian. Happ (19) stated that the spacing of the parallel marks present on the left squamosal of the same individual matched the intertooth distance of tyrannosaurids. The presence of periosteal reaction documents healing. This contrasts with the report by Farlow and Holtz (3) and again by Hone and Rauhut (20) of the same *Hypacrosaurus* fibula containing a superficially embedded theropod tooth. Absence of bone reaction precludes confident attribution to predation.

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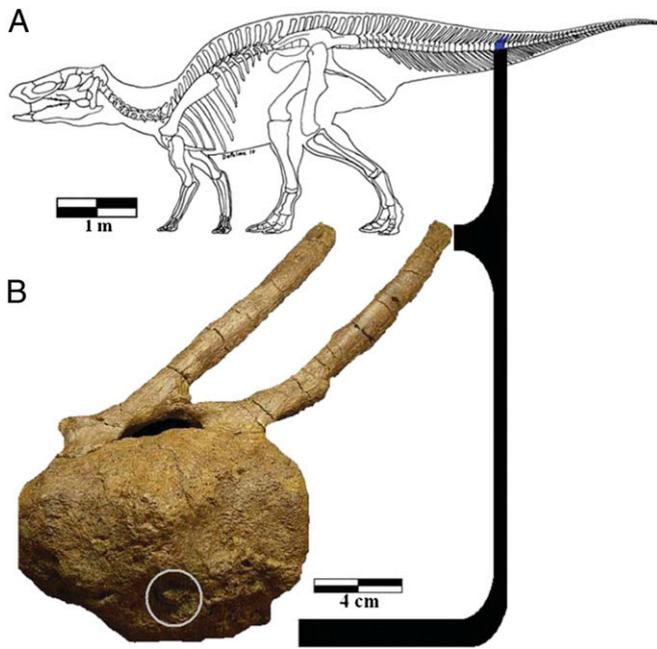


Fig. 1. Depiction of a hadrosaur skeleton showing the position in the tail of the fused vertebrae (A) and a lateral view of the affected vertebrae with the circle indicating the location of the theropod tooth (B).

Two coalesced hadrosaur (compare with *Edmontosaurus annectens*) caudal vertebrae were discovered in the Hell Creek Formation of Harding County, South Dakota (40). Archosaur fauna identified in this site include crocodiles, dinosaurs, and birds (41). Physical evidence of dental penetration and extensive infection (osteomyelitis) of the fused vertebral centra and healing (bone overgrowth) document an unsuccessful attack by a large predator. A tooth crown was discovered within the wound, permitting identification of the predator as *T. rex*. This is unambiguous evidence that *T. rex* was an active predator, fulfilling the criteria that Farlow and Holtz (3) advanced. As *T. rex* comprises between 1% and 16% of the Upper Cretaceous dinosaurian fauna in Western North America (41–45), its status as a predator or obligate scavenger is nontrivial and could have significant implications for paleoecological reconstructions of that time period. The present contribution provides unique information demonstrating the ecological role for *T. rex* as that of an active predator. Despite this documentation of predatory behavior by *T. rex*, we do not make the argument that *T. rex* was an obligate predator. Like most modern large predators (27, 45) it almost certainly did also scavenge carcasses (9, 16).

Results

The fused vertebrae are an articulated pair from the midcaudal series, estimated to have been in positions between caudals 24 and 31, of an adult hadrosaur, most likely *E. annectens* (Fig. 1 A and B). The dimensions of both vertebrae are nearly identical, with a dorsal process 15.5 cm in length and a centrum length of 5.5 cm. Although the specimen shows some abrasion caused by fluvial transport, there does not appear to have been an appreciable loss of exterior bone and it is well preserved overall. Fusion of the vertebrae was accomplished through extensive rugose syndesmophyte-like bone growth that covers the majority of the external surface of the centra (Fig. 2 A–C). This reactive bone massively overgrew the entire external surface of the two vertebrae. The articular surfaces of the centra appear to have been spared and are completely free of reactive bone. Postmortem breakage on the ventral surface of the centra indicates that the chevron could also have been fused to the centra, but had been subsequently broken off during fluvial transport. A tooth of a large theropod was situated ventrolaterally on the left side, lodged between the two vertebral centra. The tooth consists of the crown only, with no root material present. The rugose bone growth on the centra extends up to and around the embedded tooth, partly enclosing it (Figs. 1 and 2).

The theropod tooth crown is well preserved, with the broken basal portion of the tooth partially exposed (Fig. 1). Computerized tomographic (CT) scans revealed the crown height to be 3.75 cm, and visual inspection revealed the crown base length to be 2.35 cm and the crown base width 1.65 cm. Denticles are well preserved on the mesial and distal carinae (Fig. 3), and the distal basal denticle (DB) and mesial basal denticle (MB) densities are 16 per cm and 13 per cm, respectively. Comparison of the embedded tooth's dimensions and morphometric relationships with the data from the Smith et al. (46) study reveals a strong alliance with *T. rex* (Fig. 4). The tooth is indistinguishable in morphology, size, and denticle character from known *T. rex* subadults (e.g., Los Angeles County Museum–23845 and Black Hills Institute–6439). An independent comparison of the ratio of the distance from crown tip (DCT) to the incremental crown length (ICL) for *T. rex* and *Nanotyrannus*, the only two contemporaneous large-bodied and large-toothed theropods (46–49), with that of the embedded tooth places it firmly within the *T. rex* range (Fig. 3). For this study, *Albertosaurus* was added as a control. In addition, study of the embedded tooth's denticle density indicates that its DB and MB values overlap those of only one animal studied, *T. rex* (Fig. 3). Morphologic and morphometric characters of *Nanotyrannus* are sufficiently dissimilar from the embedded tooth to exclude it from candidacy for the tooth-producing taxon. Only one animal studied—*T. rex*—bears close resemblance to the tooth in question.

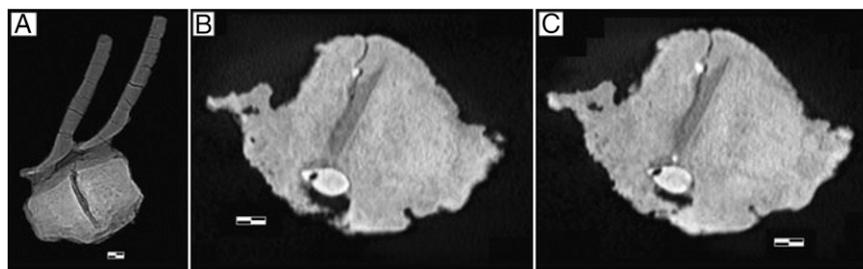


Fig. 2. CT scans of the fused hadrosaur vertebrae, showing embedded theropod tooth and reactive bone (A–C). Longitudinal slice through the fused vertebrae shows the substantial overgrowth of reactive bone on the outside of the centra, while the articular surfaces remain largely unaffected (A). Two oblique slices through the vertebrae show the embedded theropod tooth in cross-section and the reactive bone that partially surrounds it (B and C). (Scale bars: A, 20 mm and B and C, 10 mm.)



Fig. 3. Lateral view of embedded tooth crown showing well-developed blood grooves oriented obliquely toward the base and large, chisel-shaped mesial denticles typical of *T. rex* (60); (Scale bar: 5 mm.)

Discussion

The rugose structures observed on the hadrosaur vertebrae are consistent in morphology with bone growth associated with healing injuries, as observed in modern and extinct animals (Fig. 1). In modern endothermic animals, trauma to bone is followed by signs of insipient bone healing within the first several weeks. The first macroscopic evidence of bone healing in mammals can be recognized 7–10 d after the injury (50). Healing of reptilian bone is much slower (50) and takes longer in reptiles (50–53), significantly delaying opportunity for its recognition on macroscopic examination. The massive bone reaction in this report suggests survival of the injury for a significant period, perhaps even years. The injury does not appear to have contributed to the demise of this hadrosaur.

The usefulness of individual theropod teeth in determining their taxonomic affinities has been recognized by other researchers

(46, 54) and detailed, quantitative methods of examining theropod teeth have recently been developed and refined (46). The methods developed by Smith et al. (46) demonstrate the extent of the discriminating potential of theropod dental characters and enabled identification of isolated *T. rex* tooth crowns with over 96% accuracy in their study.

The localization of the tyrannosaur tooth in the midcaudal area of the hadrosaur is consistent with that noted in modern pursuit predator attacks (27, 55). Kalahari lions have been observed to initially target the hindquarters of the prey animal, in an attempt to immobilize it. This hadrosaur escaped and began to heal around the tooth lodged in its caudal vertebrae, providing evidence of the attack and the identity of the attacker. Such evidence is rare in the fossil record for good reason—prey rarely escapes. As such, it is plausible that many of the purported *T. rex* bite marks that show no healed bone are actually indicative of successful kills. What is clear is that the *T. rex* did not finish off this hadrosaur.

The fused vertebrae and embedded tooth are the result of an attack on a live hadrosaur, not the scavenging of a carcass, and represent unequivocal evidence of a predator–prey relationship (3, 33). Rugose bone growth encrusting and partially covering the embedded tyrannosaur tooth in the hadrosaur vertebrae indicates that the hadrosaur was unquestionably injured while it was alive and survived the attack long enough to partially heal. The duration of time between the attack and time of death is unknown, however healing rates from modern ectotherms and endotherms suggest that the hadrosaur could have lived from several months to perhaps a number of years after the attack (50–53). Prey animals that survive attacks by some modern predators, such as lion, hyena, and coyote attacks, frequently can

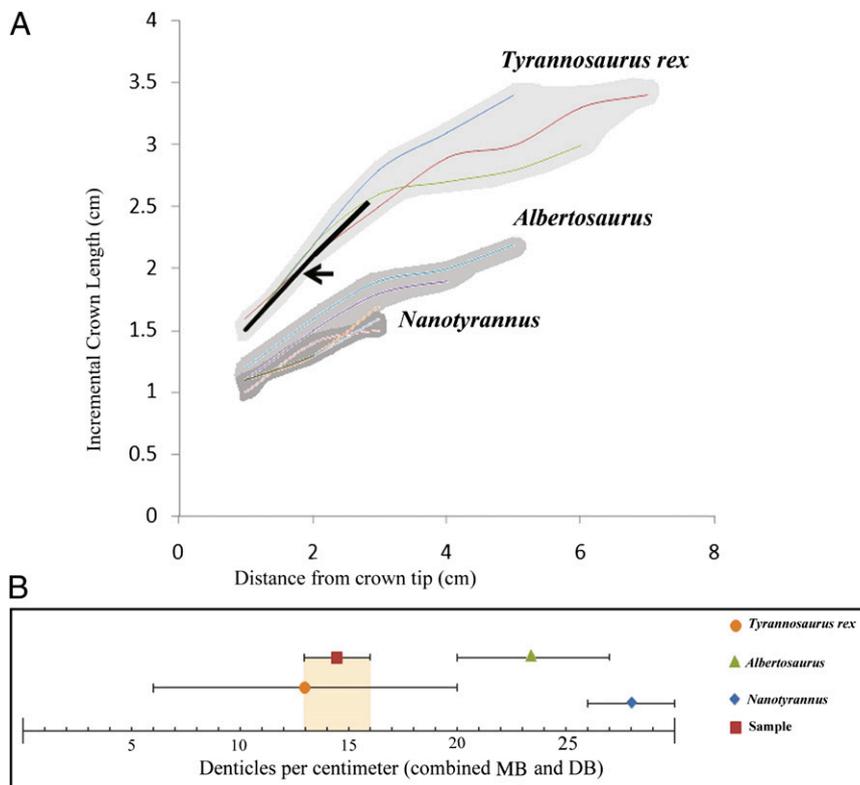


Fig. 4. Graph of tooth dimensions for *T. rex*, *Albertosaurus*, and *Nanotyrannus*, compared with that of the embedded theropod tooth (A and B). When the ICL is plotted against the DCT (A), the three examined taxa are clearly separated, with a large gap existing between *T. rex* and *Albertosaurus*, and minor overlap between *Albertosaurus* and *Nanotyrannus*. The embedded theropod tooth falls only within the region occupied by *T. rex* (bold black line in A) and does not overlap with the other two taxa. Graphed ranges of tooth denticles per cm (B) indicates a similar trend, in which the embedded theropod tooth only overlaps *T. rex* and does not match either *Albertosaurus* or *Nanotyrannus*.

survive long enough to heal (27, 55–58). Whereas the healed vertebrae demonstrate in this particular case that the attack on the hadrosaur was not consummated by a kill, they are not a sign that *T. rex* was a poorly skilled predator. Modern terrestrial predators (e.g., coyotes and lions) fail or abort between 45% and 62% of their attacks (47, 55–58).

Evidence that a *T. rex* attacked a living hadrosaur indicates predatory behavior, at least in this one instance, and elucidates our view of Western North American Upper Cretaceous paleoecology. Previous assertions that *T. rex* was exclusively a scavenger would require us to modify our reconstructions of the paleoecology to accommodate a scavenger of such significant proportions. The fact that *T. rex* engaged in predatory behavior enables a more plausible paleoecological reconstruction, suggesting an ecology similar to those observed today, such as the African savannah (27, 58).

Conclusion

We now have conclusive evidence that *T. rex* indeed engaged in predatory behavior. Whereas previously cited fossil evidence, such as isolated tooth marks, might have been easily misconstrued as the result of scavenging behavior, or predatory behavior carried out by another large theropod, our specimen includes the identities of the prey animal and the attacker and the fact that the prey was alive when attacked. Moreover, the position of the injury—the tail—suggests that *T. rex* could possibly have engaged in pursuit predation. As a significant component of the Late Maastrichtian Western North American ecology, perspectives of *T. rex*'s role as either a scavenger or predator has a profound effect on our view of the paleoecology because it is such a massive animal. As such,

our view of this large theropod as a predator enables us to speculate with more confidence on more accurate paleoecological reconstructions for Laramidia in the Late Cretaceous.

Materials and Methods

The vertebrae and tooth crown specimen are repositated at the Palm Beach Museum of Natural History (PBMNH.P.09.039). The fossils were stabilized with cyanoacrylate adhesive PaleoBond PB002 and PB100 and prepared using a Comco MB1000 micro air-abrasive unit with sodium bicarbonate powder. Particularly recalcitrant patches of matrix were removed using a PaleoTools MJ5 micro air-scribe. After preparation, the specimen was sealed with polyvinyl acetate stabilizer and later imaged by CT radiography (Siemens SOMATON Sensation 64-slice). CT scanning revealed the tooth's orientation within the vertebrae. The tooth crown is well preserved with enamel and denticles intact.

The morphology and morphometric relationships of the embedded theropod tooth in the present study were examined following the methodology of the Smith et al. (46) study. The measurements were compared with the Smith et al. (46) data, with large theropod taxa documented in the Hell Creek Formation (*T. rex* and *Nanotyrannus*), with *Albertosaurus* as an exemplar of smaller tyrannosaurids. Initially proposed by Bakker et al. (47), the taxonomic status of *Nanotyrannus* has been questioned (59) but is considered a valid taxon for this study.

The ratio of two additional sets of measurements for the embedded tooth, DC and ICL, was also examined and compared with the theropod taxa listed above. The DCT is defined in 1cm increments, and the ICL is defined as the specific crown length observed at each of the DCT increments (Fig. 1A).

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