

A CERATOPSID PELVIS WITH TOOTHMARKS FROM THE UPPER CRETACEOUS KIRTLAND FORMATION, NEW MEXICO: EVIDENCE OF LATE CAMPANIAN TYRANNOSAURID FEEDING BEHAVIOR

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Abstract—A well-preserved incomplete ceratopsid pelvis from the late Campanian of New Mexico exhibits a number of toothmarks attributed to the tyrannosaurid *Daspletosaurus*. The toothmarks are mostly simple, shallow punctures, but some “puncture and pull” marks are identified, together with possible score marks possibly made by pre-maxillary teeth. These toothmarks represent scavenging behavior by one or a number of *Daspletosaurus*. The habits of tyrannosaurids in general are characterized as being opportunistic carnivores specializing in shake-feeding.

INTRODUCTION

The anterior half of an isolated ceratopsid pelvis (SMP VP-1900) was collected in the Summer of 2005 from the De-na-zin Member of the Kirtland Formation at SMP locality 210, San Juan Basin, New Mexico. The specimen (Fig. 1A) was discovered ventral side up in a thin (<1 m) bed of medium-to-coarse grained sandstone near the base of a prominent mound. The dorsal side of the ilia rested on a mudstone-sandstone contact, and we believe that the specimen had been an isolated element that was washed in with the deposition of high energy sand.

The generic identity of the specimen is uncertain, but it may pertain to *Pentaceratops sternbergii*, the index taxon for the Kirtlandian (Sullivan and Lucas, 2006). Aside from being well-preserved, the specimen is of particular interest because of several prominent toothmarks on the ilia and on the transverse processes of the dorsal (sacral) vertebrae, which became apparent after preparation. These toothmarks provide direct evidence of predatory behavior.

Generally, direct evidence for behavior of extinct taxa is rare in the fossil record (Farlow and Holtz, 2002), but examples such as analysis of footprint assemblages (e.g., Lockley and Matsukawa, 1999) or bite marks (e.g., Erickson and Olson, 1996) are occasionally reported. More commonly, behavior is indirectly inferred from studies of functional morphology (e.g., Hutchinson and Garcia, 2002), or taphonomic occurrence (e.g., Currie, 1998). Fiorillo (1991) outlined the morphology and occurrence of tooth puncture and score marks (“bone modification features”) that might be expected on bones that had been utilized by predatory dinosaurs. Tooth-marked dinosaur bones have been noted in the literature (Hunt et al., 1994; Erickson and Olson, 1996; Chure et al., 1998; Jacobsen, 1998, 2001), but generally there is a scarcity of publications on such occurrences, possibly attributable to these features being overlooked, but also due to the relative scarcity of toothmarks in the Mesozoic record (Fiorillo, 1991).

Erickson and Olson (1996) reported on a bite-marked *Triceratops* pelvis (MOR 799). The bite marks themselves were thought to have been created by *Tyrannosaurus rex*, and this was used to assert the view that *T. rex* scavenged flesh from carcasses, at least occasionally. Here, we report the occurrence of a ceratopsid pelvis (SMP VP-1900) that also exhibits numerous toothmarks and possible score marks. Institutional abbreviations: MOR = Museum of the Rockies, Bozeman, MT; SMP = State Museum Pennsylvania, Harrisburg, PA.

DESCRIPTION

Pelvis—SMP VP-1900 (Fig. 1A) is the anterior half of a ceratopsid pelvis, consisting of the anteriormost eight fused vertebrae, and both (incomplete) ilia, estimated to be 70% complete. The antero-posterior length of the preserved portion measures approximately 68 cm with a maximum

lateral width of 79 cm across the ilia. Beyond the eighth centrum and the posterior third of the ilia, the pelvis has been eroded by subaerial exposure.

Toothmarks—Twelve definitive tooth marks have been identified, with an additional 21 possible others (Fig. 1B). These are distinct and morphologically consistent with toothmarks described elsewhere (Fiorillo, 1991; Erickson and Olson, 1996). No toothmarks show any signs of trauma or healing. Most examples are puncture marks, with only a few tentative score marks. No serration marks are observable.

Puncture marks—Apart from a single puncture on the left ilium, puncture marks are limited to the ribs and neural processes only, and are concentrated on the anteriormost two thirds of the specimen. Typically the marks show a single puncturing event that caused breakage and depression of the surrounding bone, with no associated “drag” or “score” marks. Punctures vary in size from 4 mm to 2 cm wide, typically they are about 1 cm in diameter and no deeper than 1 cm. Some punctures on the margins of sacral ribs appear to pierce through the thin flange of bone so that the total depth of tooth penetration cannot be ascertained. A deep puncture on the preserved fifth right rib is associated with a ~1 cm deep furrow (Fig. 1B,b; Fig. 2). A smaller furrow on the third preserved rib (right side) is orientated roughly parallel to this. Puncture marks on the transverse ribs on either side of the fused neural spine complex, which itself is devoid of puncture marks, are arranged in two sub-parallel lines.

Score marks—In general, tooth score marks are characterized by an initial indentation, with a subsequent, gradually-shallowing groove scored into the bone surface (e.g., Fiorillo, 1991). Such a groove often shows variable splintering in small bursts around the edges. Poor bone surface preservation can mask the presence of score marks (Buffetaut and Suteethorn, 1989). In SMP VP-1900, the surface is well-preserved, but widespread shallow cracking makes identification of score marks difficult. Nevertheless, some score marks are tentatively identifiable and these appear limited to the surfaces of the ilia. Additional score marks may be present, but those described here are limited to marks that are not associated with areas of cracking.

The left ilium bears a single score mark running for about 3 cm laterally (Fig. 1B,b; Fig. 3). The right ilium bears a similar 1.5 cm lateral score mark (Fig. 1B,c). Also on the anterior third of the right ilium is a set of four subparallel score marks that run anteroposteriorly for at least 4 cm (Fig. 1B,d); three similarly-subparallel score marks, that may represent a continuation, can be found 6 cm posterior to the first four running anteroposteriorly for an additional 1 to 4 cm (Fig. 1B,e). All these score marks are approximately 1 mm wide and no more than 1 mm deep. Initial indentations are not observable on any score marks. Also, there is no obvious shallowing of the groove (with the exception of Fig. 1B,b), so it is not possible to determine the relative direction of the tooth when the score marks were made.

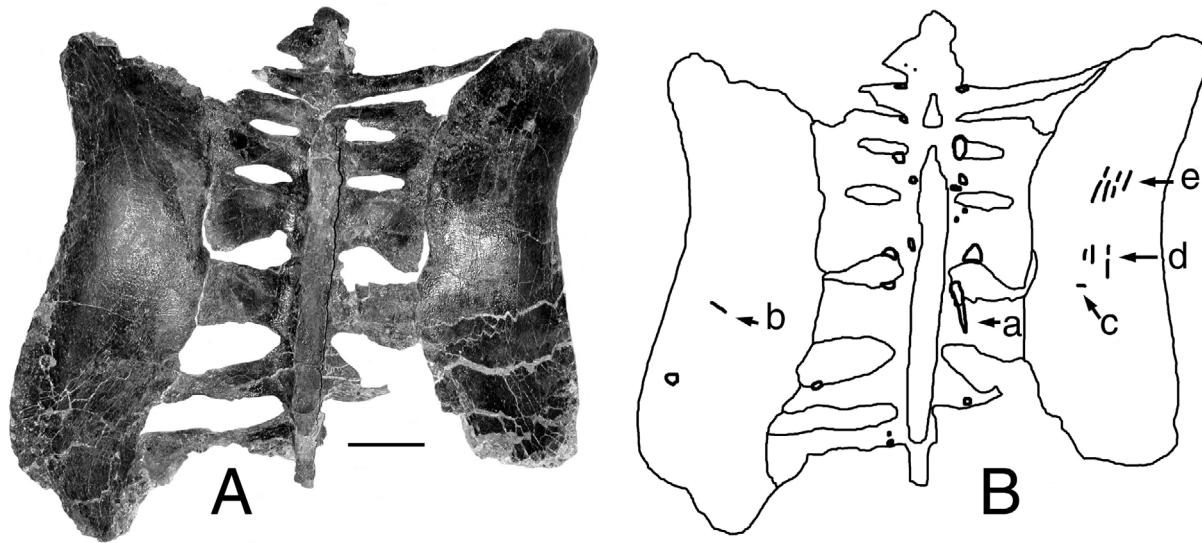


FIGURE 1. **A**, SMP VP-1900, anterior portion of ceratopsid pelvis with predatory tooth marks, from the Kirtland Formation (De-na-zin Member), San Juan Basin, New Mexico. **B**, schematic diagram of SMP VP-1900 illustrating location and shape of numerous puncture and score marks. Scores shown as single lines; punctures as enclosed circles/ovals. Notable marks are interpreted as follows: **a**, possible puncture and pull mark; **b-c**, lateral scores; and **d-e**, parallel score marks. Bar scale = 10 cm.

DISCUSSION

None of the described toothmarks show any signs of trauma or healing, supporting the hypothesis that the toothmarks were inflicted either after death or shortly beforehand. Such deep toothmarks, positioned in the center of the pelvis, would have been nearly impossible to inflict during an attack on a live animal. It is assumed here that the toothmarks therefore represent post-mortem scavenging of the carcass, which is consistent with its taphonomic occurrence in the field.

It has been suggested that, like modern carnivores, Mesozoic predators would have specifically targeted the belly and pelvis areas of carcasses, as this is where the nutritious organs are situated (Sander, 1992; Erickson et al., 1996). However, the dorsal surface of the pelvis would not have presented much meat to a potential scavenger, although thick muscle tissue is present along the neural spines. It is possible that the concentration of toothmarks in this area represents repeated attempts at biting this muscle mass by one or a number of scavengers. It is also possible that the two near parallel lines of punctures on either side of the neural spine complex represent marks created by a single strike from both sides of a jaw. However, it is difficult to envisage how an animal might bite over the top of the neural spine complex, although neural spines are relatively low in ceratopsid sacra, so this is not an anatomical impossibility. The pair of puncture marks on the preserved fifth rib (right side) might represent an example of “puncture and pull” feeding strategy (Erickson and Olson, 1996): an initial tooth incision and subsequent drag creating a shallowing groove across the bone surface (Fig. 1B,b; Fig. 2).

The shallow score marks on the ilia seem to represent a different feeding strategy than the punctures. The dorsal surface of the ilia would present very little muscle mass for feeding. It appears likely, that the dorsal score marks on the ilia were produced when the scavenger was attempting to strip flesh from the ventral side, clamping its whole jaw over the ilium, or perhaps represent marks made in the later stages of processing the carcass, when the last remaining meat was removed.

Clearly, as a scavenged carcass, all of the toothmarks need not have been made at the same time, nor by the same individual or species. However, the consistent size and linear orientation of the punctures indicate that the majority may have been created in a single feeding session by the same maker.

Discerning the identity of a toothmark maker is problematic, especially if no isolated teeth are found with the specimen (Chure et al., 1998). In their analysis of a punctured *Triceratops* pelvis, Erickson and Olson

(1996) inserted clay into a single deep puncture, producing a cast of an intruded tooth that looked remarkably similar to a crown attributed to *Tyrannosaurus rex*. The puncture marks on SMP VP-1900 are not deep enough to allow this method, but comparison of size and morphology of the puncture marks is possible.

From the known carnivorous dinosaurs of the Willow Wash local fauna (De-na-zin Member) (see Sullivan and Lucas, 2006), the 2 cm width of the largest puncture marks point to the tyrannosaurid dinosaur *Daspletosaurus* sp. While it is possible that the marks may have been made by a particularly large individual of the goniopholidid crocodylian *Denazinosuchus* (Lucas and Sullivan, 2003), isolated crocodylian teeth sufficiently large to have made such punctures are extremely rare in the De-na-zin Member in comparison to the abundance of large tyrannosaurid teeth. The narrowness of the “puncture and pull” furrow (Fig. 1B,a) is also consistent with the hypothesis that the majority of puncture marks were created by the blade-like teeth of *Daspletosaurus*; the conical teeth of goniopholidids seem ill-suited to making this sort of mark. If the parallel puncture marks represent a single bite, the jaw width and consistent size and spacing of teeth implied is inconsistent with the morphology of *Denazinosuchus*, but very similar to what is expected for marks made by the narrow snout of *Daspletosaurus*. The parallel score marks (Fig. 1B,d-e) are consistent with those expected from the premaxillary teeth of *Daspletosaurus*.

IMPLICATIONS FOR STUDIES OF TYRANNOSAURID FEEDING BEHAVIOR

Much discussion has historically surrounded the predatory capability of large theropod dinosaurs, especially the Late Cretaceous tyrannosaurids of North America and Asia (e.g., Farlow, 1976). Particular attention has been paid to adult specimens of *T. rex*, the largest, most robust, and youngest member of the clade (e.g., Horner, 1994; Horner and Lessem, 1993; Lingham-Soliar, 1998). Recent ecologic studies concerning *T. rex* have covered a broad range of subjects including morphometrics (e.g., Farlow et al., 1995), running ability (e.g., Hutchinson and Garcia, 2002) and analysis of the senses (e.g., Brochu, 2000). Regarding SMP VP-1900, the most significant research concerns tooth morphology and function.

A phylogenetic trend towards higher bodymass, a broader, more robust skull, and broader teeth is observable from basal tyrannosaurids (e.g., *Gorgosaurus*) to the most derived: *T. rex* (Currie et al., 2003). Curiously, a

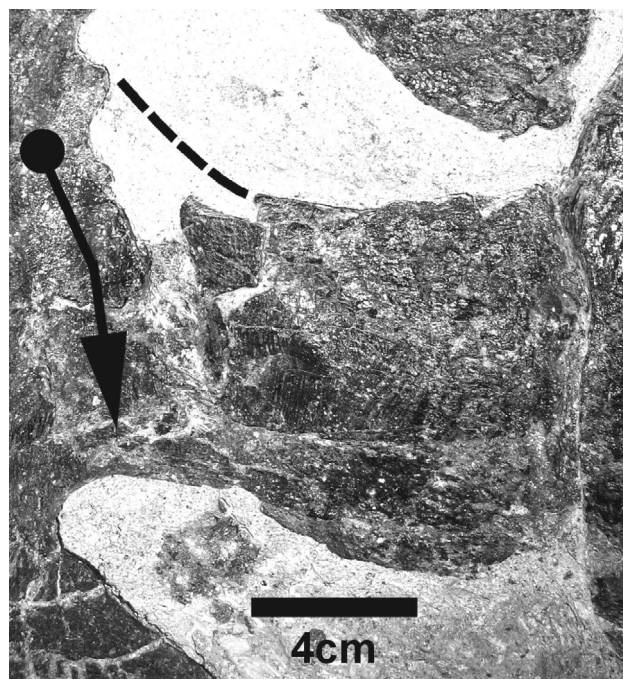


FIGURE 2. Close-up of puncture and pull mark on preserved fifth right rib (Fig. 2A). The circle and arrow are immediately left of the puncture and pull mark. The circle denotes initial puncture, subsequent drag direction and length of mark indicated by arrow. The dashed line shows original outline of sacral rib. Bar scale = 4 cm.

similar trend occurs during the ontogenetic series of *T. rex*, which develop from relatively slender toothed juveniles to broad toothed adults, possibly even losing some tooth positions in adulthood (Carr, 1999; Carr and Williamson, 2004; Holtz, pers. commun. to DWF, 2005). These subtle changes in morphology with respect to both ontogeny and phylogeny are in part responsible for the notorious difficulty in assigning isolated tyrannosaurid teeth to a specific taxon (Smith et al., 2005).

The laterally broad teeth of tyrannosaurids are considered atypical for large-bodied theropods, the typical condition were narrow blade-like teeth (e.g., *Allosaurus*). The stout morphology of tyrannosaurid teeth has led to suggestions that adult *T. rex* may have been exclusive scavengers, as they possess the broadest teeth of all (Horner, 1994; Horner and Lessem, 1993). SMP VP-1900 demonstrates that in the tyrannosaurids, bone puncturing habits predate the appearance of the exceptionally broad-toothed *T. rex* by at least 7 million years. This could be seen as support for inferring a scavenging habit for other large tyrannosaurid dinosaurs, but this interpretation is equivocal. However, SMP VP-1900 does illustrate that there is no support for the hypothesis that the broad-toothed condition most developed in adult *T. rex* evolved specifically as an adaptation towards bone puncturing. More narrow toothed tyrannosaurids also punctured bone on occasion, so another explanation must be sought.

Lingham-Soliar (1998) observed that broad teeth are present in some taxa that use only the head for prey manipulation and restraint. This is typically seen in crocodiles, but also in many extinct and extant marine taxa unable to use swimming-adapted limbs to manipulate prey (e.g., mosasaurs, orcas). Broad teeth are often accompanied by a method of prey dispatch called “shake-feeding” in which a prey item is held in the mouth and shaken violently, causing it significant wounds. Lingham-Soliar (1998) suggests that the especially large robust skull and broad teeth of *T. rex* are ideal adaptations to this habit. In further support of this, we note that the unusual presence of serrations on the entire anterior edge of the tooth would provide a bidirectional cutting surface, consistent with the shaking hypothesis. Also, the short arms of tyrannosaurids, while no use in grasping prey, would be ideal for clutching prey near the mouth (Carpenter, 2002). The suggestion of Horner (1994) and Horner and Lessem (1993) that *T. rex*

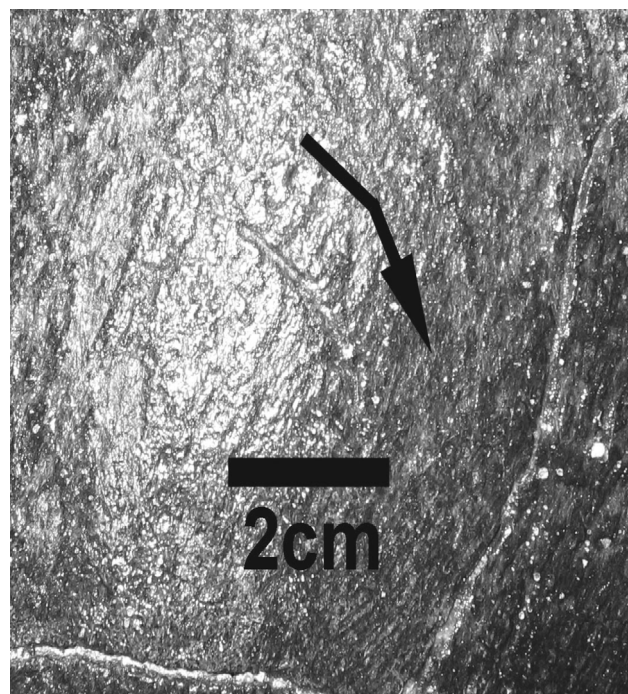


FIGURE 3. Close-up of score mark on dorsal surface of the left ilium (Fig. 1B). Arrow is immediately right of the score. Arrow shows orientation and possible direction of score. Bar scale = 2 cm.

fed differently from other large theropod dinosaurs is valid, but our interpretation here is that this reflects a shift from repeated “slash and run” predation as seen in narrow-toothed, relatively long-armed theropods, towards shake-feeding in broad-toothed, short-armed tyrannosaurids. Also, note that broad-skulled “allosaurids” are known from the Morrison Formation of North America (“*Antrodemus*”: Henderson, 1998), which may have similarly specialized in shake-feeding.

This explanation corresponds to the patterns seen in the ontogenetic and phylogenetic series. Tyrannosaurids show increased adaptations towards big-game hunting, culminating in the largest adult *T. rex*. Smaller tyrannosaurids (both juvenile, and earlier occurring species) similarly employed shake-feeding strategies but fed on smaller prey, and were more cursorial. Adult *T. rex* by contrast, preyed upon larger, slower prey. This is a good illustration of niche partitioning, with each ontogenetic stage feeding on slightly different prey, minimizing competition within a single species.

CONCLUSIONS

Toothmarks, here attributed to *Daspletosaurus*, on a ceratopsid pelvis from the upper Campanian Kirtland Formation afford us unique insight into the ecology and evolution of tyrannosaurid feeding behavior. SMP VP-1900 supports the notion that tyrannosaurids would have been at least occasional scavengers, although like most modern carnivores, tyrannosaurids would likely have been opportunistic predators: both scavenging and catching their own prey.

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