EVIDENCE FOR TRANNOSAURID FEEDING BEHAVIOR FROM HADROSAURIAN DINOSAUR REMAINS IN THE AGUJA FORMATION (UPPER CRETACEOUS), BIG BEND NATIONAL PARK, TEXAS

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ABSTRACT - Preserved bones of a large hadrosaur from the upper shale member of the Aguja Formation show extensive covering of bite marks from a tyrannosaurid dinosaur. Aside from the hadrosaur hind limb elements recovered (distal tibia, astragalus, metatarsals, and pedal phalanges), only a broken tyrannosaur tooth crown is known from the collection site (TMM 43679). All of the hadrosaur bones, even the phalanges, have bite marks on multiple sides indicating that the carcass was completely dismembered during the process of feeding. The width and depth of the bite marks suggest that they were made by one or more adult tyrannosaurs. Bite marks on the shafts of the limb bones consist mostly of long, curvilinear gouges at varied angles that do not fully penetrate the thick cortical tissue. The gouges are not in parallel series, and are compatible with 'raking' of large lateral dentary or maxillary teeth across the bone surfaces multiple times. Bite marks on the articular surfaces of the bones are instead more conical or 'U-shaped' punctures that penetrate more deeply into the cancellous tissue. These marks are consistent with bites made by anterior premaxillary teeth. The pattern of bite marks suggest that these were not inflicted during the process of subduing a prey animal, but instead during the process of dismembering a dead animal. Preservation of the hind limb elements in isolation suggest that they were removed from the carcass and brought to a separate site for feeding. The feet would not seem to be a particularly 'meaty' portion of a hadrosaur carcass, and so the thorough effort on the part of a carnivore to remove all flesh from these elements may record unusual behavior, perhaps brought about by food scarcity and desperation.

INTRODUCTION

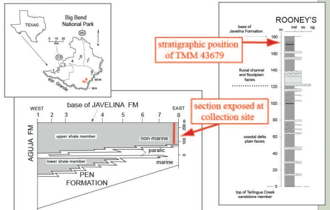
Why are bite marks of interest?

Bite marks on vertebrate bones have long been of interest in providing information about the feeding behavior of predators and scavengers and their preferred prey – information that might otherwise be unobtainable (Pobiner 2008, Erikson & Olsen 1996). The feeding behavior of large theropod dinosaurs such as tyrannosaurs have been of particular interest, and whether these animals were active predators or instead primarily scavengers has been a subject of debate (DePalma 2013, Longrich 2010).

The specimen described here, TMM 43679, includes parts of the hind limbs of a large hadrosaurian dinosaur that exhibit numerous tyrannosaur bite marks. These bite marks differ from many elsewhere attributed to tyrannosaurs, and record feeding behavior that may have differed from that typical of other tyrannosaurs.

Where was this specimen found?

Upper Cretaceous non-marine strata in the Big Bend region of Texas are divided into the Aguja Formation (Campanian) and Javelina Formation (Maastrichtian; see Fig. -). The Aguja Formation has two non-marine intervals – the lower and upper shale members. TMM 43679 was collected from the upper shale member of the Aguja Formation, just below its contact with the overlying Javelina Formation. This part of the Aguja Formation consists of fluvial channel and floodplain deposits, and is of late Campanian age – c. 77 to 72 Ma. The collection site for TMM 43679 is in southern Big Bend National Park, just north of the Rio Grande.



stratigraphic position of TMM 43679

section exposed at collection site

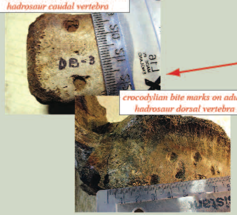
What is preserved?

TMM 43679 consists of the distal end of a hadrosaur right tibia, the right astragalus, parts of both right and left metatarsals, and a few phalanges. Additional fragments are yet to be identified, but all parts preserved belong to the distal hind limbs, and appear to pertain to a single animal. No other parts of the skeleton are represented, and apart from a broken tyrannosaur tooth crown, no other fossils are found at the site.

The hadrosaur bones show moderate pre-burial weathering; cortical bone surfaces are well preserved, but the cancellous surfaces had partly decomposed prior to fossilization. All parts of the bones have bite marks.

skeletal reconstruction of *Kritosaurus*

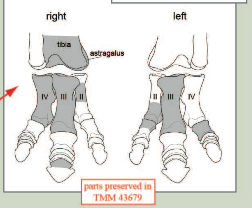
(from Paul, 1997)



crocodylian bite marks on juvenile hadrosaur caudal vertebra

crocodylian bite marks on adult hadrosaur dorsal vertebra

tyrannosaurid tooth crown preserved with TMM 43679



parts preserved in TMM 43679

Who was bitten?

Aguja hadrosaurs – The skeletal elements preserved in TMM 43679 are too fragmentary and undiagnostic to identify specifically which hadrosaur they represent. Wagner (2001) reviewed all specimens known from the upper shale member of the Aguja Formation, and determined that at least two genera are represented – *Kritosaurus* and *Angulomasticator*. Of these two it seems likely, based on its large size, that TMM 43679 could pertain to *Kritosaurus*. TMM 43679 represents a very large animal, given the length of MT III (47 cm) and distal width of the tibia (36 cm), they pertain to a hadrosaur 10 to 12 m in length, and weighing 8 to 9 metric tons.

Who was the biter?

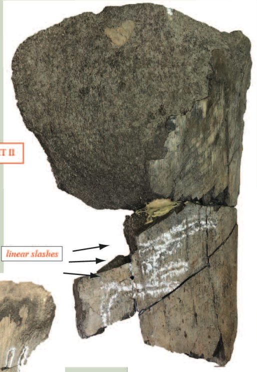
Bite mark diagnoses – Bones with crocodilian bite marks are common in the Aguja Formation – particularly in the coastal and deltaic deposits in the lower part of the formation. Most of these bite marks have been attributed to the giant crocodilian *Deinosuchus* (e.g.,Schwimmer, 2002; Lehman & Wick, 2010). Crocodilian bite marks are distinctive, and consist primarily of depressed conical punctures with nearly circular outlines, typically arrayed in linear series. Stout conical crocodilian teeth tend also to produce linear scores that are broad and U-shaped. Instead, the bite marks on TMM 43679 differ from those made by crocodilians and are instead compatible with those made by theropod dinosaurs (Longrich, 2010). The width and depth of the bite marks on TMM 43679 are too great for the marks to have been made by smaller carnivorous theropods, such as the dromaeosaurs known from the Aguja Formation (e.g., Wick et al., 2015), and instead require larger theropods. Teeth of maller theropods are laterally compressed (labial-lingual width of the crown is much less than mesial-distal width). This results in narrow, shallow, serrated bite marks that are more closely spaced (Erikson & Olsen 1996). In this case, the size and morphology of the bite marks, along with recovery of a broken tyrannosaur tooth with TMM 43679, suggest that the biter in this case was an adult tyrannosaur.

Aguja tyrannosaurs – Remains of tyrannosaurs are not common in the Aguja Formation. Specimens known thus far are too fragmentary to identify specifically, however, it seems clear that the Aguja tyrannosaur was relatively small (5 m length, 700 kg weight; see Lehman & Wick, 2013) compared to many other tyrannosaurs. Only a broken tooth crown was recovered at TMM 43679; its size and serration count are compatible with others found in the Aguja.

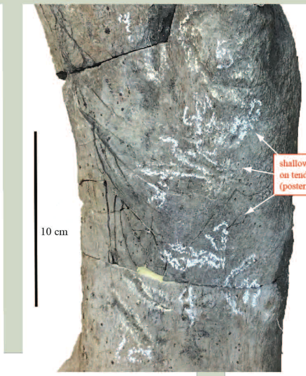
OBSERVATIONS

What do the bite marks look like?

The bite marks on TMM 43679 are randomly arrayed along the shafts and articular surfaces of all bones preserved. In particular, bite marks are concentrated on the posterior surfaces of the metatarsals; for example, on right and left MT III, there are 34 marks in total; 22 slashes and 12 punctures. The bite marks show two basic forms – (1) narrow, linear slashes and scores with a V-shaped profile, and (2) oval or U-shaped punctures. Several of the linear slashes terminate in a puncture. The linear slashes are primarily on the shafts of limb bones, and do not fully penetrate the thick cortical tissue. The punctures are primarily on the articulation surfaces, and penetrate more deeply into the cancellous tissue. Neither type of mark occurs in consistent linear or parallel series, but are instead at varied angles, lengths, and depths. None of the marks show serrated edges, but smooth continuous margins.



lateral side of right MT II

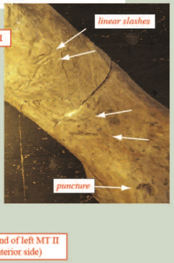


shallow slashes and punctures on tendon attachment surface (posterior side, right MT III)

posterior sides of right and left MT III

linear slashes that end in puncture marks

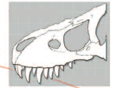
distal end of left MT II (anterior side)



posterior side of right MT III

How did the bite marks form?

The linear slashes and scores are compatible with 'raking' of large lateral dentary or maxillary teeth across the bone surfaces multiple times, and at multiple angles. The varied angles and depths may reflect the staggered arrangement of teeth along the tyrannosaur's jaws. Some of the punctures reflect penetration of these teeth as the jaws closed. Other punctures on the articulation surfaces and at tendon attachment sites instead suggest 'nipping' of the incisiform premaxillary teeth at the tips of the jaws.



'nipping' with premaxillary teeth

'raking' with staggered large lateral teeth

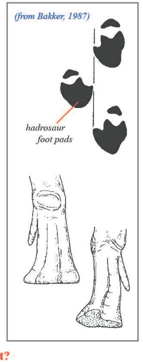
(*T. rex* maxilla drawing from Carr & Williamson, 2004)

Because the bite marks on TMM 43679 show no evidence for bone healing, and are on multiple lateral, medial, and articular surfaces of the bones, they were evidently inflicted post-mortem, and likely not a result of the struggle to subdue a living prey animal. Instead these record the process of dismembering and removing the flesh from a dead animal. The foot bones were preserved in isolation from any other parts of the skeleton, suggesting that the hind limbs had been removed from the carcass and brought to a second location for feeding. These observations are consistent with scavenging behavior.

Shallow V-shaped score marks made by teeth raked across bone surfaces without piercing through the cortical tissue have elsewhere been attributed to scavenging behavior (Pobiner, 2008).These marks differ from those produced by "puncture and pull" feeding, a predation tactic generally attributed to tyrannosaurs that relied on their great body mass and powerful neck musculature, rather than any specialized dentition (Erikson & Olsen 1996).

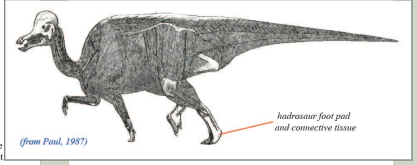
What tissue was consumed?

Hadrosaur feet were anatomically similar to bird feet, and probably had very little musculature. But, footprints and life restorations of hadrosaurs indicate that the feet had thick pads of soft-tissue beneath the ankles. The pattern of bite marks on TMM 43679 suggest that these foot pads, the connective tissue, and the cartilaginous pads on bone articulation surfaces may have been the tissue consumed by the tyrannosaur in this case. These parts of the carcass would not seem to be particularly'meaty' - however, along with the skin, tendons, and cartilage, these tissues would have been a significant source of collagen and calcium (e.g., as in chicken feet).



(from Bakker, 1987)

How 'meaty' were hadrosaur feet?



hadrosaur foot pad and connective tissue

(from Paul, 1987)

INTERPRETATION

The giant crocodylian *Deinosuchus* was probably the apex predator in Aguja habitats (e.g., Schwimmer, 2002). If so, tyrannosaurs may have been subordinate tertiary predators or scavengers in these environments. On the other hand, the hadrosaurs in this case were substantially larger (9-10 metric tons) than the local tyrannosaurs (700 kg). The great size differential may have favored scavenging rather than predation on such large animals. Young and/or smaller tyrannosaurs may have scavenged as a general strategy, or if they were active predators would have sought much smaller prey.

Clearly in this case, the tyrannosaur expended substantial effort removing what would seem to be very little flesh from otherwise unappealing parts of a carcass. If this was normal behavior, we might expect to find more reports of bitten hadrosaur foot bones - these are among the most common bones preserved of hadrosaurs in many Upper Cretaceous deposits. So, alternatively, the bite marks on TMM 43679 could instead record unusual behavior brought about by food scarcity, and so may not record 'typical' behavior.

REFERENCES

Bell, P.R. & Currie, P.J. 2010. A tyrannosaur jaw bitten by a confamilial: scavenging or fatal agonism?. Lethaia, Vol. 43, pp. 278–281

Currie PJ, Jacobsen A.R. 1995. An azhdarchid pterosaur eaten by a velociraptorine theropod. Can J Earth Sci 32:922–925

Depalma, R. A., et al. Physical evidence of predatory behavior in Tyrannosaurus rex. Proceedings of the National Academy of Sciences, vol. 110, no. 31, 2013, pp. 12560–12564.

Erickson, G.M., & K.H. Olson. "Bite marks attributable toTyrannosaurus rex: Preliminary Description and Implications." Journal of Vertebrate Paleontology, vol. 16, no. 1, 1996, pp. 175–178.

Fiorillo, A.R. 1991. Prey utilization by predatory dinosaurs. Palaeogeography, Palaeoclimatology, Palaeoecology 88:157-166

Hone., & D. Tanke. 2015. Pre- and postmortem tyrannosaurid bite marks on the remains of Daspletosaurus(Tyrannosaurinae: Theropoda) from Dinosaur Provincial Park, Alberta, Canada." PeerJ, vol. 3

Lehman, T. & S. Wick. 2013. Tyrannosauroid Dinosaurs from the Aguja Formation (Upper Cretaceous) of Big Bend National Park, Texas." Earth and Env. Sci. Trans., Royal Society of Edinburgh, 103, p. 471–485.

Longrich NR, Horner JR, Erickson GM, Currie PJ. 2010. Cannibalism in Tyrannosaurus rex. PLoS ONE 5(10): e13419.

Paul, G. 1987. The science and art of restoring the life appearance of dinosaurs and their relatives. In Dinosaurs Past & Present, Vol II, p. 5-49, Los Angeles Co. Museum Publ.

Paul, G. 1997. Dinosaur models: the good, the bad, and useing them to estimate the mass of dinosaurs. In Dinofest International, p. 129-154, Philadelphia Acad. Nat. Sci. Publ.

Pobiner, Briana. 2008. Paleoecological information in predator tooth marks. Journal of Taphonomy, vol. 6, no. 3-4, p. 373–397

Schwimmer, D., 2010. Bite marks of the giant crocodylian Deinosuchus on Late Cretaceous (Campanian) bones. New Mexico Museum of Natural History and Science, Bulletin. 51. 183-190.