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 the southern part of Big Bend National Park, just north of the Rio Grande.

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 articulation surfaces had partly decomposed prior to fossilization. All parts of the hadrosaur bones have bite marks.

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 smaller 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; it's size and serration count are compatible with others found in the Aguja.

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 the tendon attachment sites instead suggest 'nipping' of the incisiform premaxillary teeth at the tips of the jaws.

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 deeding. 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 a 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. 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).

Interpretation

The giant crocodilian *Deinosuchus* was probably the apex predator in the Aguja habitats (e.g., Schwimmer, 2002). If so, tyrannosaurs may have been the 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

1. Bell, P.R. & Currie, P.J. 2010: A tyrannosaur jaw bitten by a confamilial: scavenging or fatal agonism?. Lethaia, Vol. 43, pp. 278–281
2. Currie PJ, Jacobsen AR (1995) An azhdarchid pterosaur eaten by a velociraptorine theropod. Can J Earth Sci 32:922–925
3. 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., doi:10.1073/pnas.1216534110
4. Erickson, Gregory M., and Kenneth H. Olson. "Bite Marks Attributable ToTyrannosaurus Rex: Preliminary Description and Implications." *Journal of Vertebrate Paleontology*, vol. 16, no. 1, 1996, pp. 175–178., doi:10.1080/02724634.1996.10011297
5. Fiorillo, A. R. 1991. Prey utilization by predatory dinosaurs. Palaeo-geography, Palaeoclimatology, Palaeoecology 88:157-166
6. Hone, Dwe, and Dh Tanke. "Pre- and Postmortem Tyrannosaurid Bite Marks on the Remains OfDaspletosaurus(Tyrannosaurinae: Theropoda) from Dinosaur Provincial Park, Alberta, Canada." PeerJ, vol. 3, Sept. 2015, doi:10.7717/peerj.885
7. Lehman, Thomas M., and Steven L. Wick. "Tyrannosauroid Dinosaurs from the Aguja Formation (Upper Cretaceous) of Big Bend National Park, Texas." Earth and Environmental Science Transactions of the Royal Society of Edinburgh, vol. 103, no. 3-4, 2012, pp. 471–485., doi:10.1017/s1755691013000261.
8. Longrich NR, Horner JR, Erickson GM, Currie PJ (2010) Cannibalism in Tyrannosaurus rex. PLoS ONE 5(10): e13419. doi:10.1371/journal.pone.0013419
9. Pobiner, Briana. "Paleoecological Information in Predator Tooth Marks." Journal of Taphonomy, vol. 6, no. 3-4, 5 Mar. 2008, pp. 373–397
10. Schwimmer, David. (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.