

Physical evidence of predatory behavior in *Tyrannosaurus rex*

Robert A. DePalma II^a, David A. Burnham^{b,1}, Larry D. Martin^{b,2}, Bruce M. Rothschild^b, and Peter L. Larson^c

^aDepartment of Paleontology, Palm Beach Museum of Natural History, Ft. Lauderdale, FL 33306; ^bDivision of Vertebrate Paleontology, University of Kansas Biodiversity Institute, Lawrence, KS 66045; and ^cBlack Hills Institute of Geological Research, Inc., Hill City, SD 57745

Edited by Mark A. Norell, American Museum of Natural History, New York, NY, and accepted by the Editorial Board May 21, 2013 (received for review September 27, 2012)

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.

Author contributions: R.A.D., D.A.B., L.D.M., and B.M.R. designed research; R.A.D., D.A.B., L.D.M., B.M.R., and P.L.L. performed research; R.A.D., D.A.B., B.M.R., and P.L.L. analyzed data; and R.A.D., D.A.B., L.D.M., and B.M.R. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. M.A.N. is a guest editor invited by the Editorial Board.

¹To whom correspondence should be addressed. E-mail: dinosaur@ku.edu.

²Deceased March 9, 2013.

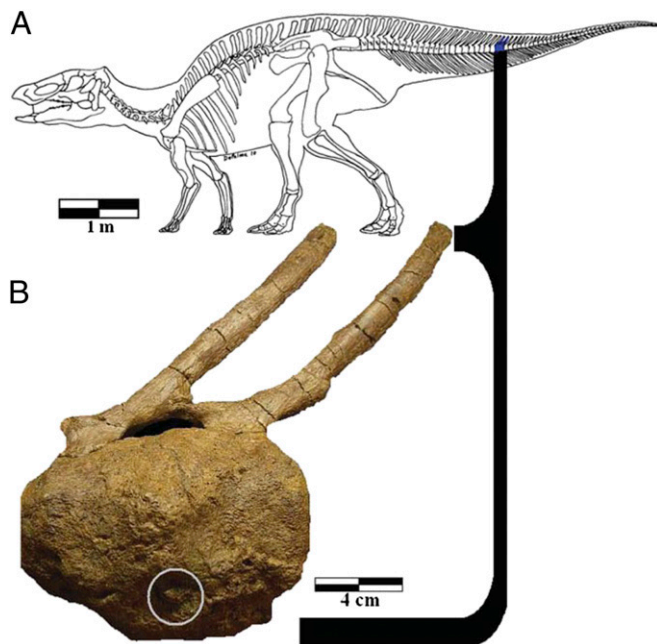


Fig. 1. Depiction of a hadrosaur skeleton showing the position in the tail of the fused vertebrae (A) and a lateral view of the affected vertebrae with the circle indicating the location of the theropod tooth (B).

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.

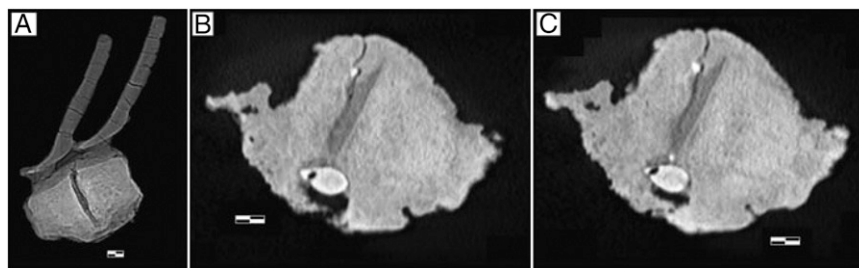


Fig. 2. CT scans of the fused hadrosaur vertebrae, showing embedded theropod tooth and reactive bone (A–C). Longitudinal slice through the fused vertebrae shows the substantial overgrowth of reactive bone on the outside of the centra, while the articular surfaces remain largely unaffected (A). Two oblique 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

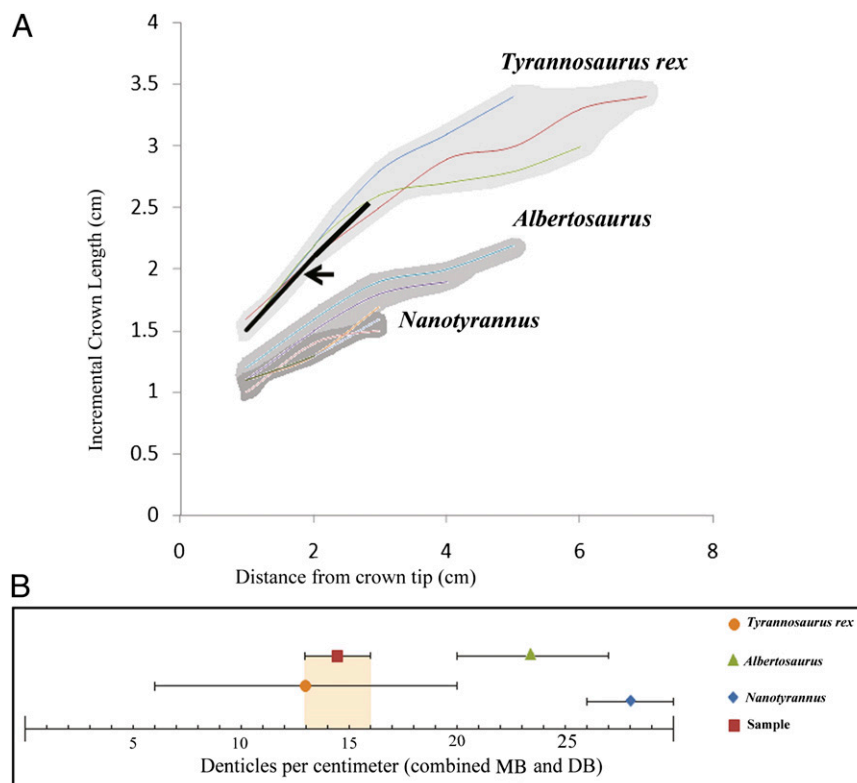


Fig. 4. Graph of tooth dimensions for *T. rex*, *Albertosaurus*, and *Nanotyrannus*, compared with that of the embedded theropod tooth (A and B). When the ICL is plotted against the DCT (A), the three examined taxa are clearly separated, with a large gap existing between *T. rex* and *Albertosaurus*, 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 1 cm increments, and the ICL is defined as the specific crown length observed at each of the DCT increments (Fig. 1A).

ACKNOWLEDGMENTS. We thank M. Schumacher of Lawrence Memorial Hospital (Lawrence, KS) for facilitating and performing the CT examination, G. Erickson for his insightful comments, and G. Woodford.

- Bishop GA (1975) *The Study of Trace Fossils*, ed Frey RW (Springer, New York), pp 261–281.
- Erickson GM, Olson KH (1996) Bite marks attributable to *Tyrannosaurus rex*: Preliminary description and implications. *J Vert Paleont* 16(1):175–178.
- Farlow JO, Holtz TR (2002) The fossil record of predation in dinosaurs. *Paleontological Society Papers* 8:251–266.
- Happ J, Carpenter K (2008) *Tyrannosaurus rex, the Tyrant King (Life of the Past)*, eds Carpenter K, Larson P (Indiana Univ Press, Bloomington, IN), pp 355–368.
- Happ JW, Morrow CM (1997) Bone modification of subadult *Triceratops* (Dinosauria: Ceratopsidae) by crocodylian and theropod dining. *J Vert Paleont* 17 (Supplement 3):51A.
- Jacobsen AR (1998) Feeding behavior of carnivorous dinosaurs as determined by tooth marks on dinosaur bones. *Hist Biol* 13:17–26.
- Bakker RT (1986) *The Dinosaur Heresies* (William and Morrow, New York).
- Brusatte SL, et al. (2010) Tyrannosaur paleobiology: New research on ancient exemplar organisms. *Science* 329(5998):1481–1485.
- Currie PJ (1997) *The Complete Dinosaur*, eds Farlow JO, Brett-Surman MK (Indiana Univ Press, Bloomington, IN), pp 216–233.
- Fiorillo AR (1991) Prey bone utilization by predatory dinosaurs. *Palaeogeogr Palaeoclimatol Palaeoecol* 88:157–166.
- Horner JR, Goodwin MB, Myhrvold N (2011) Dinosaur census reveals abundant *Tyrannosaurus* and rare ontogenetic stages in the Upper Cretaceous Hell Creek Formation (Maastrichtian), Montana, USA. *PLoS ONE* 6(2):e16574, 10.1371/journal.pone.0016574.
- Larson PL, Wolberg DL, Stump E, Rosenberg GD (1997) The king's new clothes: A fresh look at *Tyrannosaurus rex*. *Dino Fest International, Proceedings of a Symposium sponsored by Arizona State University*, eds Wolberg DL, Stump E, Rosenberg GD (Academy of Natural Sciences, Philadelphia), pp 65–71.
- Paul GS (1988) *Predatory Dinosaurs of the World: A Complete Illustrated Guide* (Simon and Schuster, New York).
- Ruxton GD, Houston DC (2003) Could *Tyrannosaurus rex* have been a scavenger rather than a predator? An energetics approach. *Proc Biol Sci* 270(1516):731–733.
- Holtz TR (2008) *Tyrannosaurus rex the Tyrant King*, eds Larson P, Carpenter K (Indiana Univ Press, Bloomington, IN), pp 371–398.
- Ryan MJ, Vickaryous MK (1997) *Encyclopedia of Dinosaurs*, eds Currie PJ, Padian K (Academic, San Diego, CA), pp 169–174.
- Carpenter K (1998) Evidence of predatory behavior by carnivorous dinosaurs. *Aspects of Theropod Paleobiology*, eds Perez-Moreno BP, Holtz TJ, Sanz JL, Mortalla J (Gaia: Revista de Geociencias, Museu Nacional de Historia Natural, Lisbon, Portugal), pp 135–144.
- Varricchio DJ (2001) Gut contents from a Cretaceous tyrannosaurid: Implications for theropod dinosaur digestive tracts. *J Paleontol* 75:401–406.
- Happ JW (2003) Peristole reaction to injuries of the supraorbital horn and squamosal of an adult *Triceratops* (Dinosauria: Ceratopsidae). *J Vert Paleont* 23 (Supplement 3):59A.
- Hone DW, Rauhut OW (2010) Feeding behavior and bone utilization by theropod dinosaurs. *Lethaia* 43:232–244.
- Thulborn RA, Wade M (1984) Dinosaur trackways in the Winton Formation (Mid-Cretaceous) of Queensland. *Mem Queensl Mus* 21:413–517.
- Maxwell WD, Ostrom JH (1995) Taphonomy and paleobiological implications of *Tenontosaurus-Deinonychus* associations. *J Vert Paleont* 15:707–712.
- Lockley M, Meyer C, Siber H-J, Pabst B (1998) Theropod tracks from the Howe Quarry, Morrison Formation, Wyoming. *Mod Geol* 23:309–316.
- Christians JP (1992) *Taphonomy and Sedimentology of the Mason Dinosaur Quarry, Hell Creek Formation (Upper Cretaceous), South Dakota*, Master's thesis (Univ of Wisconsin, Madison, WI), 91 pp.
- Horner JR (1994) *Dino Fest Paleontological Society Special Publication 7*, eds Rosenberg G, Wolberg D (Indiana Univ Press, Bloomington, IN), pp 157–164.
- Lambe LB (1917) The Cretaceous theropodous dinosaur *Gorgosaurus*. *Mem Geol Surv Can* 100:1–84.
- Stuart CT, Stuart MD (1997) *The Larger Mammals of Africa* (Struik Publishers, Cape Town, South Africa).
- Zelenitsky DK, Therrien F, Ridgely RC, McGee AR, Witmer LM (2011) Evolution of olfaction in non-avian theropod dinosaurs and birds. *Proc Biol Sci* 278(1725):3625–3634.
- Jacobs LF (2012) From chemotaxis to the cognitive map: The function of olfaction. *Proc Natl Acad Sci USA* 109(1 Suppl 1):10693–10700.
- Erickson GM, et al. (1996) Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones. *Nature* 382:706–708.
- Bates KT, Falkingham PL (2012) Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics. *Biol Lett* 8(4):660–664.
- Williamson TE (1996) *Brachychampsia sealeyi*, sp. nov. (Crocodylia, Alligatoroidea), from the Upper Cretaceous (Lower Campanian) Menefee Formation, northwestern New Mexico. *J Vert Paleont* 16:421–443.
- Lebedev OA, Mark-Kurik E, Karatjütë-Talimaa VN, Lukševičs E, Ivanov A (2009) Bite marks as evidence of predation in early vertebrates. *Acta Zool* 90(Supplement 1): 344–356.
- Currie PJ, Jacobsen AR (1995) An azhdarchid pterosaur eaten by a velociraptorine theropod. *Can J Earth Sci* 32:922–925.
- Brain CK (1981) *The Hunters or the Hunted? An Introduction to African Cave Taphonomy* (Univ of Chicago Press, Chicago).
- Fastovsky DE, Smith JB (2004) *The Dinosauria*, eds Weishempel D, Dodson P, Osmolska H (Univ of California Press, Berkeley, CA), pp 614–626.
- Jacobsen AR (2001) *Mesozoic Vertebrate Life*, eds Tanke D, Carpenter K (Indiana Univ Press, Bloomington, IN), pp 58–63.
- Sereno P, Novas FE (1993) The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *J Vert Paleont* 13:451–476.
- Tanke D, Currie P (1998) Head-biting behavior in theropod dinosaurs: Paleopathological evidence. *Aspects of Theropod Paleobiology*, eds Perez-Moreno BP, Holtz TJ, Sanz JL, Mortalla J (Gaia: Revista de Geociencias, Museu Nacional de Historia Natural, Lisbon, Portugal), pp 167–184.
- DePalma RA (2010) *Geology, Taphonomy, and Paleoecology of a Unique Upper Cretaceous Bonebed Near the Cretaceous-Tertiary Boundary in South Dakota*, Master's thesis (Univ of Kansas, Lawrence, KS).

41. White PD, Fastovsky DE, Sheehan PM (1998) Taphonomy and suggested structure of the dinosaurian assemblage of the Hell Creek Formation (Maastrichtian), eastern Montana and western North Dakota. *Palaios* 13(1):41–51.
42. Lehman TM (1987) Late Maastrichtian paleoenvironments and dinosaur biogeography in the Western Interior of North America. *Palaeogeogr Palaeoclimatol Palaeoecol* 60:189–217.
43. Russell D, Manabe M (2002) *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, eds Hartman JH, Johnson KR, Nichols DJ, GSA Special Paper 361 (The Geological Society of America, Inc., Boulder, CO), pp 169–176.
44. Bartlett JA (2004) *Taphonomy, Geology, and Paleocology of the Sandy Site, an Exceptional Assemblage in the Maastrichtian Hell Creek Formation of South Dakota*. Master's thesis (North Carolina State Univ, Raleigh, NC).
45. Eloff FC (1964) On the predatory habits of lions and hyaenas. *Koedo* 7:105–113.
46. Smith JB, Vann DR, Dodson P (2005) Dental morphology and variation in theropod dinosaurs: Implications for the taxonomic identification of isolated teeth. *Anat Rec A Discov Mol Cell Evol Biol* 285(2):699–736.
47. Bakker RT, Currie PJ, Williams M (1985) *Nanotyrannus*, a new genus of pigmy tyrannosaur from the Latest Cretaceous of Montana. *Hunteria* 1(5):1–29.
48. Larson PL (2008) *Tyrannosaurus rex, the Tyrant King*, eds Larson P, Carpenter K (Indiana Univ Press, Bloomington, IN), pp 102–128.
49. Witmer LM, Ridgely RC (2009) New insights into the brain, braincase, and ear region of tyrannosaurs (Dinosauria, Theropoda), with implications for sensory organization and behavior. *Anat Rec (Hoboken)* 292(9):1266–1296.
50. Pritchard JJ, Ruzicka AJ (1950) Comparison of fracture repair in the frog, lizard and rat. *J Anat* 84(3):236–261.
51. Frye FL (1981) *Biomedical and Surgical Aspects of Captive Reptile Husbandry (1)* (Krieger Publishing Company, Malabar, FL).
52. Katsura Y (2004) Paleopathology of *Toyotamaphimeia machikanensis* (Diapsida, Crocodylia) from the Middle Pleistocene of central Japan. *Hist Biol* 16:93–97.
53. Robertson DR (1969) The ultimobranchial body of *Rana pipiens*. X. Effect of glandular extirpation on fracture healing. *J Exp Zool* 172(4):425–441.
54. Currie PJ, Fiorillo AR (1994) Theropod teeth from the Judith River Formation (Upper Cretaceous) of south-central Montana. *J Vert Paleont* 14(1):74–80.
55. Stander PE (1992) Foraging dynamics of lions in a semi-arid environment. *Can J Zool* 70:8–21.
56. Truett JC (1979) Observations of coyote predation on mule deer fawns in Arizona. *J Wildl Manage* 43(4):956–958.
57. Gese EM, Grothe S (1995) Analysis of Coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. *Am Midl Nat* 133(1):36–43.
58. Kingdon J (1997) *The Kingdon Field Guide to African Mammals* (Princeton Univ Press, Princeton).
59. Carr TD (1999) Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). *J Vert Paleont* 19:497–520.
60. Currie PJ, Rigby JK, Jr., Sloan RE (1990) Theropod teeth from the Judith River Formation of southern Alberta, Canada. *Dinosaur Systematics: Perspectives and Approaches*, eds Carpenter K, Currie PJ (Cambridge Univ Press, Cambridge, MA), pp 107–125.