A TYRANNOSAUR (DINOSAURIA; THEROPODA; TYRANNOSAURIDAE) FROM THE LATE CRETACEOUS (MAASTRICHTIAN) HAREBELL FORMATION OF YELLOWSTONE NATIONAL PARK, WYOMING

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Abstract—In the 1960s, United States Geological Survey (USGS) geologists working in the Late Cretaceous (Maastrichtian) Harebell Formation in the Big Game Ridge area of Yellowstone National Park, Wyoming, collected the first known dinosaur fossil from this iconic park. Consisting of a single shed theropod tooth, the fossil was previously identified as a "deinodont" dinosaur, now known as a tyrannosaur. However, this fossil was long tucked away in the USGS museum collection and nearly forgotten. A recent National Park Service paleontological resource inventory (PRI) rediscovered the specimen record and it is now part of the Smithsonian Paleobiology Collections. Morphological characters and geologic distribution of Maastrichtian tyrannosaurs designate the first dinosaur identified from Yellowstone National Park, Wyoming, as a juvenile cf. *Tyrannosaurus* sp.

INTRODUCTION

The majestic environments we see at Yellowstone National Park, in northwestern Wyoming and adjoining areas of eastern Idaho and southern Montana, have an abundance of wildlife distributed throughout the park. These environments support large mammalian apex predators, such as gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and mountain lions (*Puma concolor*), that have become iconic for the park. Recent National Park Service paleontological resource inventories (PRI) have demonstrated that Yellowstone also has an extensive fossil record documenting ancient faunas from the Cambrian to the Quaternary, which contained their own unique predators (Santucci, 1998; Tweet et al., 2013). For example, the Carboniferous and Permian rocks of Yellowstone contain a diverse record of chondrichthyans (sharks and kin) (Hodnett et al., 2022). However, our PRI has uncovered that USGS geologists collected a tooth in the 1960s of a carnivorous theropod dinosaur from the type section of the Late Cretaceous Harebell Formation near Mount Hancock in the southern region of the park, representing the first known dinosaur identified from Yellowstone National Park.

THE YELLOWSTONE "DEINODONT" FROM THE HAREBELL FORMATION

During the 1960s, the USGS conducted geologic mapping surveys of the Yellowstone National Park and Teton regions, which found Late Cretaceous to Paleocene fossils in strata that would later be designated the Harebell Formation and Pinyon Conglomerate. Most of the vertebrate fossils encountered in these units were from outside the boundaries of Yellowstone National Park, including partial dinosaur remains in the Harebell Formation (Love 1973; Love and Keefer 1975) and an isolated ceratopsian tooth, later identified as *Leptoceratops* sp., from 150 feet above the base of the Pinyon Conglomerate (McKenna and Love 1970). However, while mapping the type section of the Harebell Formation near Mount Hancock in Yellowstone National Park in 1966, USGS geologist Joseph Leonard Weitz, part of a field team under John D. Love, collected a shed tooth of a theropod dinosaur from a claystone bed. The specimen was identified initially by G. Edward Lewis (1966; Chapler, 1967), of the USGS Paleontology and Stratigraphy Branch in Denver, Colorado, as an isolated tooth of a "carnivorous 'dinosaur' (Reptilia, Order Saurischia, Suborder Theropoda)" and referred it to the family "Deinodontidae" (*sensu* Matthew and Brown 1922) (G. E. Lewis, USGS, written communication to J. D. Love, 11-4-1966). "Deinodontidae" was rejected by Russell (1970) in favor of Tyrannosauridae due to the lack of diagnostic material for the former, and more widespread usage of the latter family group. Communication between Lewis and Love dated November, 1966 (Fig. 1) acknowledged that the "miserable reptile tooth" was significant as the first definitive dinosaur fossil to be discovered in Yellowstone National Park, and would be important for future interpretation of the park's natural resources. This isolated tooth would later be mentioned only in a few publications on the Harebell Formation (Chapler, 1967; Love 1973; Love and Keefer 1975); Harris et al. (1996) is the only published record that corrected the identification of this tooth as belonging to a tyrannosaur, but without describing or figuring the specimen. This fossil occurrence has also largely been ignored in surveys of dinosaurian faunas for the Harebell Formation (Weishampel et al., 2004). Here we provide the first descriptive assessment of the Yellowstone "deinodont," the first dinosaur fossil to be described from Yellowstone National Park (Fig. 2).

MATERIALS AND METHODS

The specimen described here was collected by USGS geologist Joseph Leonard Weitz in 1966. The tooth had the field number W-66-1-8A and was eventually catalogued into the United States Geological Survey Paleontology collection in Denver as specimen D704. It resided there until the collection's transfer to the Paleobiology Collections of the Smithsonian's National Museum of Natural History in 2021, where it was given the catalogue number USNM PAL 768805. Photographs were made using an Apple iPhone 12, and measurements made with digital calipers. Figures were edited and generated with Adobe Photoshop 2023 and Adobe Illustrator 2023, respectively.

Institutional Abbreviations: LACM, Natural History Museum of Los Angeles County, Los Angeles, CA**; USNM PAL**, National Museum of Natural History Paleobiology Collections, Smithsonian Institution, Washington, DC.

GEOLOGIC SETTING

The Yellowstone tyrannosaur tooth was collected from

November 16, 1966

AIRMAIL

Dr. Edward Lewis
P & S Branch
U.S. Geological Survey
Federal Center, Building 25
Denver, Colorado 80225

Dear Ed:

Thanks very much for all the work you did on my miserable reptile tooth. I'm sorry that we couldn't have gotten more and better material. Nevertheless, your identification is quite significant, for as far as I know, this is the first dinosaur fragment to have come from Yellowstone Park. Even if it is not of much scientific interest, I am sure the fact that it demonstrates dinosaurs roamed the Yellowstone area is of public interest. Therefore, I would appreciate it if you would send a copy of your report on the tooth to Mr. John M. Good, Chief Park Naturalist, Yellowstone National Park, Wyoming 83020. He has been most helpful to the Survey on the Park project, is a delightful individual, a competent geologist, and because of his official cooperation, we try to keep him informed of discoveries that can be used in his interpretation of the Park. Perhaps you may wish to include it as an item of interest in your report to the Director.

Please extend my best wishes to Jane and my thanks again for your gracious hospitality.

Sincerely yours,

J. D. Love

cc: DRF
Geol. Div. file
Br. file

FIGURE 1. Letter dated November 16, 1966 from J. D. Love to Dr. G. Edward Lewis which acknowledges Lewis's identification of the Yellowstone tyrannosaur tooth as the first dinosaur fossil to be discovered in Yellowstone National Park.

an approximately 3-meter-thick olive drab, gray-and-tan weathering claystone, 700 m above the base of the Harebell Formation on Big Game Ridge near the southern boundary of Yellowstone National Park, Wyoming (Love, 1973). The Harebell Formation overlies the Bacon Ridge Sandstone and is capped by the Pinyon Conglomerate. It is characterized by beds of sandstones, claystones, siltstones, and conglomerates. The depositional setting is considered to be primarily freshwater terrestrial with some incursions of marine or brackish waters, with streams flowing from east and northeast to the southeast into and across the Jackson Hole area from the Targhee uplifts (Love, 1973). Fossils are common throughout the Harebell Formation, including abundant leaves and mollusks (Love, 1973). Love (1973) lists the clams *Sphaerium* and *Eupera*, freshwater snails *Physa* or *Bulinus*, an unidentified high-spiral gastropod, and the land snail *Pseudocolumna*. Additional vertebrate specimens include an amioid fish, a plethodontid salamander, alligatoroid teeth, ceratopsian teeth, ornithopod teeth, and an edentulous hadrosaurian dentary (Love 1973). Four-toed theropod tracks (*Saurexallopus lovei*) collected from thick sandstone slabs are known from southeast of Yellowstone National Park in the Bridger-Teton Wilderness area (Harris et al., 1996; Harris, 1997). The age of the Harebell Formation was placed by Love (1973) as Maastrichtian based on the fossils. Harris et al. (1996) collected paleomagnetic age data from the Harebell Formation in the Bridger-Teton Wilderness area, south of Yellowstone National Park. These paleomagnetic samples ranged from 70.3 to 68.2 Ma, partly overlapping an early-late Maastrichtian age (Harris et al., 1996). This date range makes the Harebell Formation slightly older than the Hell Creek, Lance, Scollard, Frenchman, and other units containing *Tyrannosaurus* (Fowler, 2017).

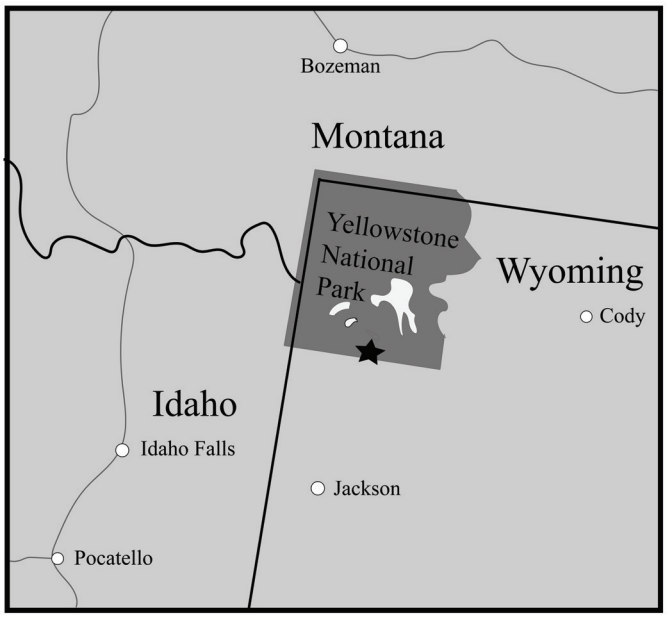


FIGURE 2. Map of Yellowstone National Park and the approximate location of Big Game Ridge (star).

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Theropoda Marsh, 1881
FAMILY Tyrannosauridae Osborn, 1906
GENUS *Tyrannosaurus* Osborn, 1905
cf. *Tyrannosaurus* sp.

Occurrence—Harebell Formation, Big Game Ridge, Yellowstone National Park, Wyoming.

Material— USNM PAL 768805, right distal premaxillary tooth.

Description— A single shed tyrannosaurid premaxillary tooth, missing the apical tip (Fig. 3). Preserved crown height is 18.6 mm, mesiodistal width is 9.6 mm, and the labiolingual width is 7.6 mm. The mesial margin recurves distally, with the distal margin being slightly concaved distally. The labial margin is rounder mesiodistally than the lingual margin, giving a roughly D-shaped cross section. The mesial carina is offset lingually from mesiodistal midline of the crown and they terminate approximately 1/8th above the crown base. The distal carinae are lingually directed from the mesiodistal midline of the crown, and the carina extends to the crown base. Serrations are generally rounded with a low apex, separated from one another by a relatively deep groove. Serration density for the mesial and distal serration is two per millimeter. Based on the size, this tooth mostly like derived from a juvenile or young adolescent individual (Fig. 4).

Remarks—Lateral teeth of dromaeosaurs and tyrannosaurs are superficially similar when they are approximately the same size, and records of large dromaeosaurids are known elsewhere in the Maastrichtian of North America (DePalma et al., 2015; Jasinki et al., 2020). However, there are important differences in these dentitions, with dromaeosaurs having proportionately larger distal serrations compared to the mesial serrations and tyrannosaurs (particularly *Tyrannosaurus*) having proportionately stouter teeth (Currie et al., 1990; Norell and Makovicky, 2004). Currie et al. (1990) noted that young tyrannosaur teeth tend to be stout in general proportions when compared to dromaeosaurs and troodontids but are laterally more compressed compared to adult tyrannosaur teeth. The isolated tooth from Yellowstone National Park can be confidently placed

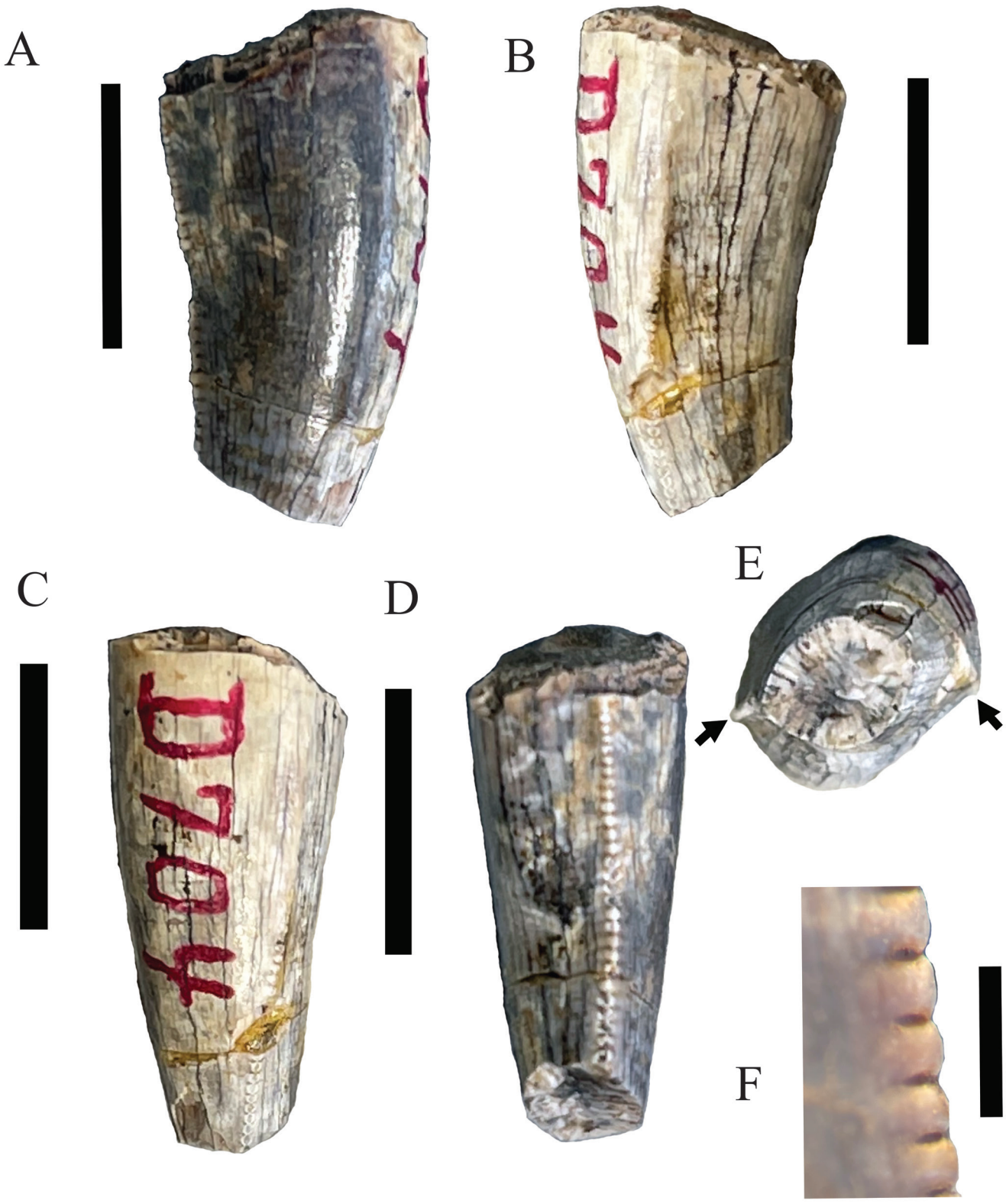


FIGURE 3. USNM PAL 768805, a juvenile distal premaxillary tooth of cf. *Tyrannosaurus* sp. A, labial view, B, lingual view, C, mesial view, D, distal view, E, occlusal view with arrows pointing to the mesial (right) and distal (left) carina, F, close-up of the distal serrations. Scale A-E equal 1 cm, F equal 1 mm.



FIGURE 4. A reconstructed mounted skeleton of a juvenile *Tyrannosaurus rex* (LACM 28471) at the Natural History Museum of Los Angeles County, representing the approximate size and age of the Yellowstone tyrannosaur. Photo by JP Hodnett.

as a tyrannosaurid theropod premaxillary tooth by its relatively stout, D-shaped cross-section and low, rounded serrations that are the same size on the mesial and distal carinae (Currie et al., 1990; Carr and Williamson, 2004). The D-shape derives from the lingual placement of the mesial and distal carinae, typical of *Tyrannosaurus* premaxillary teeth (Smith, 2005) as well as those of other tyrannosaurids.

USNM PAL 768805 bears diagnostic features of tyrannosaurid teeth, but not of particular taxa within Tyrannosauridae. Therefore, our tentative identification of this specimen as an example of *Tyrannosaurus* is based largely on our current understanding of the distribution of tyrannosaur taxa within the Maastrichtian of the upper Cretaceous in western North America. Previously, small North American tyrannosaur fossils of Maastrichtian age were argued to represent small-sized taxa, such as *Aubysiodon* or *Nanotyrannus* (Leidy, 1860; Molnar, 1978, 1980; Bakker et al., 1988; Molnar and Carpenter, 1989; Lehman and Carpenter, 1990; Larson, 2013). Carr (1999) and Carr and Williamson (2004) undertook an extensive review of the known small late Maastrichtian western North American tyrannosaur specimens, concluding that these small tyrannosaur taxa in fact represent various growth stages of *Tyrannosaurus* rather than separate taxa. Carr and Williamson (2004) also concluded that *Tyrannosaurus* was the only tyrannosaurid represented in the late Maastrichtian dinosaur assemblages of western North America. Though a few continue to argue that some specimens are a small distinct tyrannosaur taxon (e.g., Larson, 2013), most recent work on Late Cretaceous tyrannosaur ontogeny supports the theory that the small-bodied examples of late Maastrichtian North American tyrannosaurs are juvenile *Tyrannosaurus* (Tsuihiji et al., 2011; Voris et al., 2022). Equally important, and unlike the tyrannosaurids present in earlier (Campanian) faunas of the region, *Tyrannosaurus* seems to have been the only tyrannosaurid present across a wide geographic area of western North America. Thus, it is most probable that the small tyrannosaurid premaxillary tooth from the Harebell Formation of Yellowstone National Park represents a juvenile *Tyrannosaurus*.

DISCUSSION AND CONCLUSIONS

The juvenile tyrannosaur tooth (USNM PAL 768805) from Big Game Ridge in Yellowstone National Park is potentially the first record of *Tyrannosaurus* from the Maastrichtian Harebell Formation. This would add to the known geologic distribution and stratigraphic range of *Tyrannosaurus* in western North America, which currently spans the Denver, Ferris, Frenchman, Hell Creek, Javelina, Laramie, Lance, McRae, North Horn, Scollard, and Willow Creek formations (Larson, 2008; Johnson, 2008). However, further tyrannosaur specimens will be needed from the Harebell Formation to fully validate this occurrence.

There is strong potential for the Harebell Formation within Yellowstone National Park to yield more paleontological data through additional future surveys, which would enrich our knowledge of Late Cretaceous life in this under-documented region of Wyoming. A preliminary NPS paleontological assessment survey in 2022 in the Big Game Ridge region documented fossil resources within the area, but the majority of these were plants and mollusks (JST and CCV, personal observations, 2022). Dinosaur fossils found outside of Yellowstone National Park in the Harebell Formation include indeterminate remains of hadrosaurs and ceratopsians (Love, 1973), and these forms could also be found within the park. What is currently certain is that this little “miserable reptile tooth” demonstrates the power of in-depth and determined natural resource inventory work to reveal forgotten knowledge and natural treasures that enrich our national narrative of ancient life in the United States. It seems befitting that the first dinosaur fossil to be identified and described from our first national park likely belongs to our nation’s most iconic and popular dinosaur genus, *Tyrannosaurus.*

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REFERENCES

Bakker R. T., Williams, M., and Currie, P. J., 1988, *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana: Hunteria, v. 1, p. 1–30.

Carr, T. D., 1999, Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria): Journal of Vertebrate Paleontology, v. 19, p. 497-520.

Carr, T. D. and Williamson, T. E., 2004, Diversity of late Maastrichtian Tyrannosauridae (Dinosauria: Theropoda) from western North America: Zoological Journal of the Linnean Society, v. 142, p. 479-523.

Chapler, A., 1967, Dinosaurs in Yellowstone Park: U.S. Geological Survey, Proffesional Paper 575-A, p. A120.

Currie, P. J., Rigby, J. K., and Sloan, R. E., 1990, Theropod teeth from the Judith River Formation of Southern Alberta, Canada; *in* Carpenter, K. and Currie, P. J., eds., Dinosaur Systematics, Approaches and Perspectives: Cambridge University Press, p. 107-125.

DePalma, R. A., Burnham, D. A., Martin, L. D., Larson, P. L. and Bakker, R. T., 2015, The first giant raptor (Theropod: Dromaeosauridae) from the Hell Creek Formation: Paleontological Contributions, no. 14, p. 1-16.

Fowler, D.W., 2017, Revised geochronology, correlation, and dinosaur stratigraphic ranges of the Santonian-Maastrichtian (Late Cretaceous) formations of the Western Interior of North America: PLoS ONE 12(11): e0188426. https://doi.org/10.1371/journal.pone.0188426

Harris, J. D., Johnson, K. R., Hicks, J., and Tauxe, L., 1996, Four-toed theropod footprints and a paleomagnetic age from the Whetstone Falls Member of the Harebell Formation (Upper Cretaceous: Maastrichtian), northwest Wyoming: Cretaceous Research, v. 17, p. 381-401.

Harris, J. D., 1997, Four-toed theropod footprints and a paleomagnetic age from the Whetstone Falls Member of the Harebell Formation (Upper Cretaceous: Maastrichtian), northwestern Wyoming: a correction: Cretaceous Research, v. 18, p. 139.

Hodnett, J.-P. M., Tweet, J. S. and Santucci, V. L., 2022, The occurrence of fossil cartilaginous fishes (Chondrichthyes) within the parks and monuments of the National Park Service: New Mexico Museum of Natural History and Science, Bulletin 90, p. 183-208.

Jasinski, S. E., Sullivan, R. M., and Dodson, P., 2020, New dromaeosaur dinosaur (Theropoda, dromaeosauridae) from New Mexico and biodiversity of dromaeosaurids at the end of the Cretaceous: Scientific Reports, v. 10:5105 | https://doi.org/10.1038/s41598-020-61480-7 1

Johnson, K., 2008, How old is *T. rex*? Challenges with the dating of terrestrial strata deposited during the Maastrichtian stage of the Cretaceous Period; *in* Larson, P. and Carpenter, K., eds., *Tyrannosaurus rex*, The Tyrant King. Indiana University Press, Bloomington, p. 63-66.

Larson, N. L. 2008. One hundred years of *Tyrannosaurus rex*: the skeletons; *in* Larson, P. and Carpenter, K., eds., *Tyrannosaurus rex,* The Tyrant King. Indiana University Press, Bloomington, p. 1-56.

Larson, P., 2013, The case for *Nanotyrannus*; *in* Parrish, J. M., Molnar, R. E., Currie, P. J. and Koppelhus, E. B., eds., Tyrannosaurid Paleobiology: Indiana University Press, Bloomington, p. 15-53.

Lehman, T. M. and Carpenter, K., 1990, A partial skeleton of the tyrannosaurid dinosaur *Aublysodon* from the Upper Cretaceous of New Mexico: Journal of Paleontology, v. 64, p. 1026–1032.

Leidy J., 1860, Extinct vertebrates from the Judith River and Great Lignite formations of Nebraska: Transactions of the American Philosophical Society, v. 11, p. 139–154.

Lewis, G. E., 1966, Report on Referred Fossils: USGS unpublished specimen report, Denver Colorado, 1 p.

Love, J. D., 1973, Harebell Formation (Upper Cretaceous) and Pinyon Conglomerate (Uppermost Cretaceous and Paleocene), northwestern Wyoming: U. S. Geological Survey, Professional Paper 734-A, 54 p.

Love, J. D. and Keefer, W. R., 1975, Geology of sedimentary rocks in southern Yellowstone National Park, Wyoming: U. S. Geological Survey, Professional Paper 729-D, 60 p.

Matthew, W. D. and Brown, B., 1922, The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta: Bulletin of the American Museum of Natural History, v. 48, p. 367-385.

McKenna, M. C. and Love, J. D., 1970, Local stratigraphic and tectonic significance of *Leptoceratops*, a Cretaceous dinosaur in the Pinyon Conglomerate, northwestern Wyoming: U. S. Geological Survey, Professional Paper 700-D, p. 55-61.

Molnar R. E., 1978, A new theropod dinosaur from the upper Cretaceous of central Montana: Journal of Paleontology, v. 52, p. 73–82.

Molnar R. E., 1980, An albertosaur from the Hell Creek Formation of Montana. Journal of Paleontology 54: 102–108.

Molnar R. E. and Carpenter K. 1989. The Jordan theropod (Maastrichtian, Montana, U.S.A.) referred to the genus *Aublysodon*: Geobios, v. 22, p. 445–454.

Norell, M. and Makovicky, J. 2004. Dromaeosauridae; *in* Weishampel, D.B., Dodson, P., and Osmolska, H., eds., The Dinosauria, Second Edition: University of California Press, Berkley, p. 196-209.

Osborn, H. F., 1905, *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs: Bulletin of the American Museum of Natural History, v. 21, p. 259-265.

Osborn, H. F., 1906, *Tyrannosaurus*, Upper Cretaceous carnivorous dinosaur. (Second communication): Bulletin of the American Museum of Natural History, v. 22, p. 281-296.

Russell, D.A., 1970, Tyrannosaurs from the Late Cretaceous of Western Canada: National Museum of Natural Sciences, Publications in Palaeontology 1, p. 1-32.

Santucci, V. L., 1998, The Yellowstone Paleontological Survey: Yellowstone Center for Resources, National Park Service, Yellowstone National Park, Wyoming, YCR-NR-98-1.

Smith, J. B., 2005, Heterodonty in *Tyrannosaurus rex*: implications for the taxonomic and systematic utility of theropod dentitions: Journal of Vertebrate Paleontology, v. 25, p. 865-887.

Tsuihiji, T. Watabe, M., Tsogtbaatar, K., Tsubamoto, T., Barsbold, R., Suzuki, S., Lee, A. H., Ridgely, R. C., Kawahara, Y., and Witmer, L. M., 2011, Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia: Journal of Vertebrate Paleontology, v. 31, p. 497-517.

Tweet, J. S., Santucci, V. L., and Connors, T., 2013, Paleontological resource inventory and monitoring: Greater Yellowstone Network: Natural Resource Report NPS/GRYN/NRTR—2013/794. National Park Service, Fort Collins, Colorado.

Voris, J. T., Zelenitsky, D. K., Therrien, F., Ridgely, R. C., Currie, P. J. and Witmer, L. M., 2022, Two exceptionally preserved juvenile specimens of *Gorgosaurus libratus* (Tyrannosauridae, Albertosaurinae) provide new insight into the timing of ontogenetic

changes in tyrannosaurids: Journal of Vertebrate Paleontology. DOI: 10.1080/10.1080/02724634.2021.2041651

Weishampel, D. B., Barrett, P. M., Coria, R.A., Le Loeuff, J., Xing, X., Xijin, Z., Sahni, A., Gomani, E. M., and Noto, C. R., 2004, Dinosaur Distribution; *in* Weishampel, D.B., Dodson, P., and Osmolska, H., eds., The Dinosauria, Second Edition: University of California Press, Berkley, p. 517-606.