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THEROPOD BITE MARKS ON DINOSAUR BONES: INDICATIONS OF A SCAVENGER, PREDATOR OR BOTH?; AND THEIR TAPHONOMIC IMPLICATIONS

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Abstract— Three nearly complete, isolated vertebrae, and a right humerus of a sub-adult hadrosaurine (Ornithopoda: Hadrosaurinae), all from separate individuals and from the Late Cretaceous (late Campanian) Hunter Wash local fauna (Fruitland Formation [Fossil Forest Member] and Kirtland Formation [Hunter Wash Member]), San Juan Basin, New Mexico, bear distinctive bite marks. These bite marks vary in size and shape, suggesting that different species of theropods, or possibly different ontogenetic individuals of a single species, were feeding on the carcasses pertaining to these individual elements. The isolated vertebrae suggest post-mortem bites, probably from scavenging behavior, whereas the bite marks on the humerus may have been inflicted during predation. Based on the bite mark traces, it appears that all bite marks were made by tyrannosauroids of different ontogenetic stages and/or different species.

INTRODUCTION

Fossil vertebrates have been known from the Upper Cretaceous strata of the San Juan Basin for over a century (e.g., Brown, 1910). Ongoing fieldwork continues to further our knowledge of the fossil vertebrates from the Kirtlandian land-vertebrate "age" in New Mexico (e.g., Sullivan and Lucas, 2003, 2006). Although most fossils recovered are single, disarticulated elements, numerous dinosaur taxa are known from these strata, including hadrosaurids, ceratopsids, ankylosaurids, pachycephalosaurids and theropods (e.g., Sullivan and Lucas, 2006). Multiple theropod taxa are known from the Upper Cretaceous strata of the San Juan Basin. These include troodontids, dromaeosaurids, ornithomimids, and tyrannosauroids (e.g., Lucas, 1981, 1993; Lucas et al., 1987, 2000; Sullivan and Lucas, 2000, 2003, 2006; Sullivan, 2006; Carr and Williamson, 2010; Jasinski et al., 2011; Jasinski, 2015).

Fossil traces left by vertebrates on fossil bones have been noted in various previous studies (e.g., Fiorillo, 1991; Erickson and Olson, 1996; Carpenter, 1998; Chure et al., 1998; Tanke and Currie, 1998; Rogers et al., 2003; Carpenter et al., 2005; Fowler and Sullivan, 2006; Holtz, 2008; Peterson et al., 2009; Hone and Rauhut, 2010; Hone and Watabe, 2010; Longrich et al., 2010; Rivera-Sylva et al., 2012). Bite marks on theropod fossils are more rare, but have also been discussed in the literature (e.g., Tanke and Currie, 1998; Rogers et al., 2003; Peterson et al., 2009; Bell and Currie, 2010; Longrich et al., 2010). Additionally, traces attributed to bite marks on specimens from the Campanian strata of New Mexico have previously been mentioned by Fowler and Sullivan (2006) and Hunt and Lucas (2015).

Here we describe four additional specimens from the Campanian of the San Juan Basin, New Mexico that bear bite marks attributed to theropod dinosaurs. One is the humerus of a sub-adult hadrosaurine with multiple marks indicating feeding behavior of a large theropod believed to be a tyrannosauroid. Additionally, three isolated vertebrae also possess bite marks on both sides of their centra. One of these vertebrae is identified as a hadrosaur. However, the other two are identified as theropod vertebrae that have been fed on by other theropod dinosaurs. The likely culprit for all of these is a large theropod, however, differing size classes may lead to differing identifications of the biting theropods, with possibilities ranging from multiple theropod taxa, to different ontogenetic stages of a single theropod taxon.

Institutional Abbreviations: **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque; **SMP**, The State Museum of Pennsylvania, Harrisburg.

SPECIMENS BEARING THEROPOD BITE MARKS

Material: NMMNH P-70319, nearly complete sub-adult hadrosaurine (Ornithopoda: Hadrosaurinae) right humerus (Fig. 1).

Locality: NMMNH L-9273, Ah-shi-sle-pah WSA.

Formation/Member: Kirtland Formation (Hunter Wash Member).

Description: The right humerus (NMMNH P-70319, Fig. 1) is nearly complete and measures 34.5 cm in length. The bone is fractured in several places and has been fully restored. The main shaft of the humerus is well preserved, while the distal and proximal ends are slightly eroded.

In caudal view (Fig. 1A), the shaft bears nine prominent traces of scored (or drag) bite marks, and two lesser bite marks, along the ridge that extends distally, separating the muscle scars of the latissimus dorsi and that of the lateral border. The largest bite mark measures 2 cm long (in total length) while the smallest and shallowest bite mark measures 0.7 cm long. The distal portion of the humerus is marked by a series of what appear to be *en echelon* compression fractures. In cranial view (Fig. 1D), the proximal end is slightly fractured by postmortem compression, while the distal end is marked by diagonal hair-like fractures and what appear to be at least five to eleven scored (or drag) bite marks. All the bite marks seem to be simple score (or drag) marks with the exception of one V-shaped mark on the caudal (posterior) side (Fig. 1B).

Discussion: NMMNH P-70319 is identified as a juvenile hadrosaurine based on the size and narrow nature of the deltopectoral crest. Our comments will focus on the bite marks on the caudal side of the humerus as we are uncertain about whether or not the traces on the distal end of the cranial side are in fact bite marks. This uncertainty is due to the fact that the distal end of the cranial side of the humerus is badly weathered and the nature of the marks cannot be accurately determined. We have arbitrarily numbered the bite marks from the distal to proximal ends #1-7 along the ridge and #8-9 that are offset from the ridge that are on the body of the deltopectoral crest (Fig. 1C).

The three most distinct bite marks are located distally on the ridge of the deltopectoral crest. Bite mark #1 measures 1.9 cm in length, bite mark #2, the largest bite mark on the bone, measures 2 cm and bite mark #3 measures 1.4cm. All three are simple score marks. Bite marks #2 and #3 form a V-shaped mark that connects cranially. Most interestingly, all three bite marks exhibit indentations of the denticles suggesting predation by a theropod with large, course denticles on the tooth. Bite marks #4-7 are sub-parallel to each other and are near uniformly spaced. These marks are all slightly less than a centimeter in length. Taking into account the lesser bite marks as well, there may have been at least three separate biting events that took place during feeding. As there is no evidence of re-healing and the placement of the marks is located at an area that would be damaged during feeding but not during an attack, these marks are believed to have all been post-mortem events that occurred during feeding either from the predator that took down the hadrosaurine or another individual that scavenged the carcass at a later point.

Material: SMP VP-2206, Hadrosauridae indeterminate, ?proximal caudal vertebra (Fig. 2).

Locality: SMP loc. 421 (Alamo Mesa [southwest]), Bisi-De-na-zin Wilderness.

Formation/Member: Kirtland Formation (Hunter Wash Member).

Description: SMP VP-2206 represents a dorsal vertebra (questionably anterior) from an indeterminate hadrosaurid (Fig. 2).

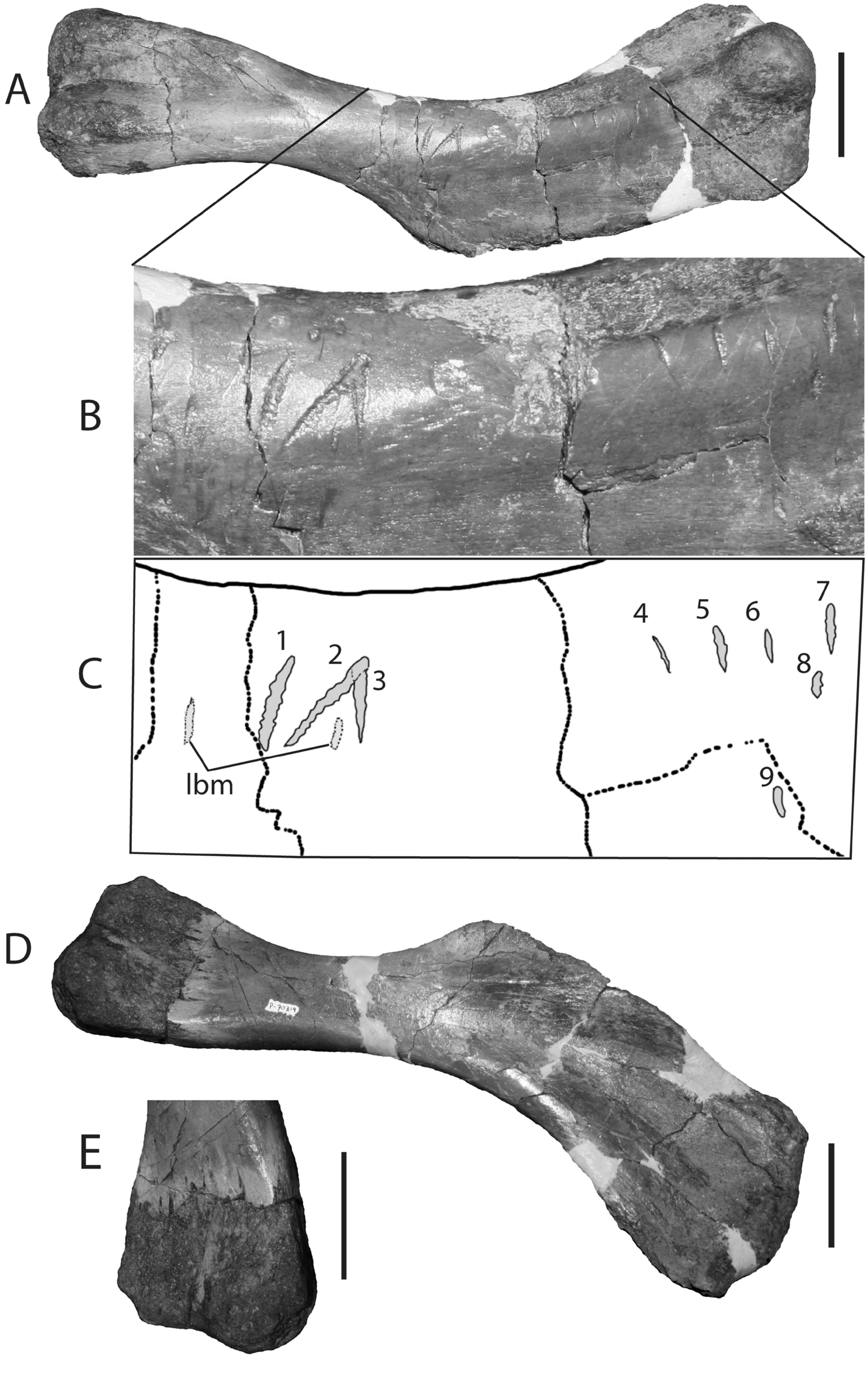

FIGURE 1. Hadrosaurinae indeterminate, NMMNH 70319, nearly complete sub-adult right humerus in: **A**, posterior (caudal) view; **B**, magnified bite mark area on ridge; **C**, illustration of same, highlighting bite marks (in grey); **D**, anterior (cranial) view; and **E**, magnified distal end (cranial view) showing problematic bite marks which are vertical grooves situated along the weathered section of the bone. **Abbreviation: lbm**, lesser bite mark. Bar scales = 5 cm.

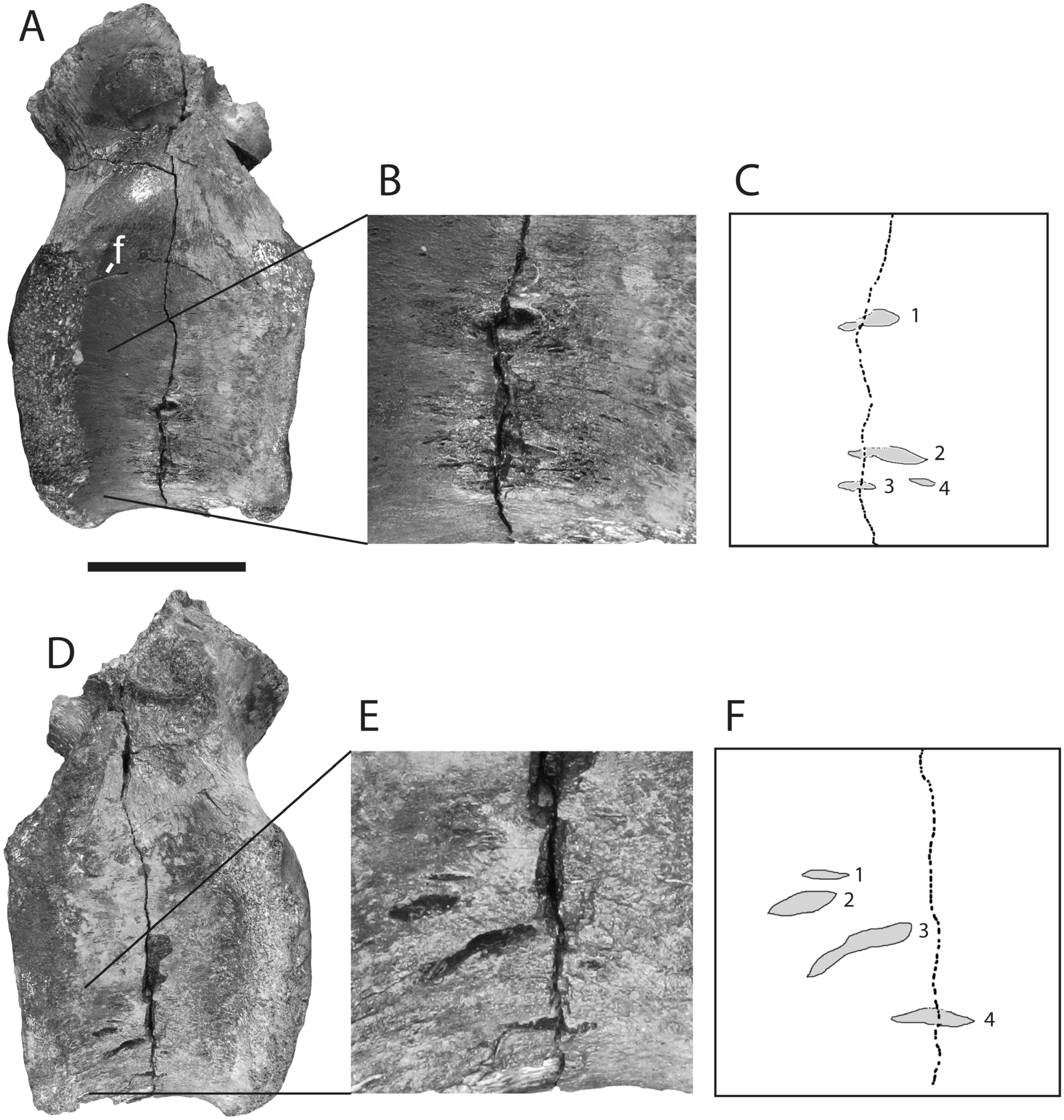

FIGURE 2. Hadrosauridae indeterminate, SMP VP-2206, adult ?anterior dorsal vertebra in: **A**, left lateral view; **B**, magnified portion showing traces of bite marks; **C**, illustration of same, highlighting the bite marks (in grey); **D**, right lateral view; **E**, magnified portion showing the bite marks; and **F**, illustration of same, highlighting the bite marks (in grey). **Abbreviation**: **f,** furrow. Bar scale = 5 cm.

The centrum has a maximum length (craniocaudally) of 9.7 cm and a maximum height (measured along the midline at the caudal end) of 9.0 cm. The preserved portion of the vertebra has a maximum height (measured from the ventral base to the top of the preserved portion of the neural spine) of 17.5 cm and a width (measured midway through the centrum) of 6.6 cm. The dimensions (height to the base of the neural canal by maximum width) of the anterior surface of the centrum are 9.3 cm by 8.1 cm, while those of the posterior surface are 9.0 cm by 8.2 cm. The neural canal is preserved and has dimensions of 3.3 cm (height) by 2.9 cm (width). The centrum is slightly compressed laterally, while the anterior end is slightly convex and the posterior end is slightly concave. The centrum, particularly the anterior end, has a general heart-like shape. Dorsal to the centrum lie portions of the neural arch and neural spine. Parts that are preserved include small portions of the prezygapophyses, hyposphene, centrodiapophyseal laminae, infradiapophyseal fossae, and remnants of the postzygapophyses.

Bite marks are present on both the left and right sides of the centrum. The left side has five bite marks (Fig. 2A-C), with the largest 1.3 cm in total length, and the smallest 0.5 cm long. Spacing between the traces (from dorsal to ventral) is 2.0 cm and 0.3 cm, with bite marks

#3 and #4 being roughly congruent and anterior-posterior of each other. Bite marks #1 and #2 each have small ridges running perpendicular to the axis of the bite mark within each. Bite mark #1 has a rounded rim rather than sharp demarcation of its edges. On the left side there is a small furrow on the anterolateral portion of the centrum (Fig. 2A), it measures 1.3 cm in total length.

The right lateral side has four to questionably five traces of bite marks, with the largest 1.5 cm (Fig. 2F.3) and the smallest 0.5 cm (Fig. 2F.1). Spacing between the bite marks (from dorsal to ventral) is 0.2 cm, 0.6 cm, and 1.1 cm, respectively. Bite mark #3 may represent two bite marks, as there is a change in the morphology of the trace between its anterior and posterior portions.

Discussion: Based on the morphology, the specimen (SMP VP-2206) is identified as a hadrosaurid dorsal vertebra (probably anterior), based on its heart-shaped centrum (Horner et al., 2004). The neural arch is fused, suggesting it is from a mature individual.

The traces of bite marks are of particular note on the lateral sides of the vertebra (SMP VP-2206). The broken edges around the marks are not flaked, and the internal edges are distinct from what would be expected if the marks were simple broken surfaces. All also present similar morphology in agreement with the puncture mark the apex of a tooth would make, or the bite-and-drag marks a tooth would make. Indeed, the majority of the potential bite marks have sharp, distinct rims which also implies the traces are not vertebral foramina. While both sides distinctly possess four bite marks, there may possibly be a fifth on the right side. On the left side there is a large gap between bite marks #1 and #2. This may be due to a missing tooth (teeth) within the jaw of the biting theropod as the spacing between bite marks #2 and #3 (and #4) is far smaller (see description above). As noted above, bite marks #1 and #2 on the left side possess perpendicular ridges within. These ridges could be associated with the broken apex of a tooth. Both distal points on either side of the ridges are more distinct. A tooth with a broken or split apex may then have two smaller apices, and produced two distinct distal points. Bite mark #1, as noted above, has a rounded rim, which may be indicative of a wound that had at least partially healed, or was in the process of healing at the time of death. However several other interpretations are more likely, including; it may a bite mark from a tooth with slightly different morphology that left such a trace, or potentially that it is a genetic or pathologic artifact that is superficially similar to a bite mark, or finally that it may some kind of vertebral foramen. All the marks on the left side are puncture marks, with no scoring or dragging. The furrow on the dorsolateral portion of the left lateral side of the centrum is believed to represent either insect or bacterial damage and not represent the feeding trace or drag mark from a theropod tooth. On the right side, the bite marks are all puncture marks, and are mostly relatively small other than bite mark #3. As noted above, bite mark #3 may actually be two distinct bite marks, as there is an inconsistent symmetry to the dorsal rim. If it represents two bite marks, it may suggest two different biting events. However, if it a single bite mark, then it represents a scoring or “bite-and-drag” mark. Due to the size of the larger bite marks, the culprit is believed to be a tyrannosauroid, similar to *Bistahieversor* (Carr and Williamson, 2010).

Material: SMP VP-2407, sub-adult theropod caudal vertebra (?10-?15) (Fig. 3).

Locality: SMP loc. 450 (Target 8/“Sleepy Grass arroyo”).

Formation/Member: Fruitland Formation (Fossil Forest Member).

Description: SMP VP-2407 is a middle caudal vertebra (?10-?15) from an indeterminate sub-adult theropod (Fig. 3). The centrum has a maximum length (craniocaudally) of 10.6 cm, maximum height (measured along the midline at the caudal end) of 8.6 cm, and a minimum height (measured midway through the centrum) of 7.6 cm. The width (measured midway through the centrum) is 4.5 cm. The centrum is slightly compressed laterally, with the anterior portion fractured. The dimensions (height to the base of the neural canal by maximum width) of the anterior surface of the centrum are 7.0 cm by 5.8 cm, while those of the posterior surface are 6.2 cm by 4.6 cm. The caudal end of the centrum has been eroded and the outer compact bone has been lost, exposing the less dense inner core (= cancellous bone) of the vertebra. The pre- and postzygapophyses, as well as the neural spine, are missing. The neural arch is unfused, thus the sutures are visible. The base of the neural canal is preserved, with the remnants of the neural arch making up its walls.

Bite marks are present on both the left and right sides of the centrum. The left side has five traces of bite marks, with the largest trace 1.5 cm in total length, and the smallest 0.6 cm. Spacing between the traces (from dorsal to ventral) is 1.0 cm, 0.4 cm, 0.1 cm, and 0.8 cm, respectively. The right side has five traces of bite marks, with the largest trace 1.7 cm in total length, and the smallest 0.7 cm. Spacing between the bite marks (from dorsal to ventral) is 0.3 cm, 0.5 cm, 0.7 cm, and 0.6 cm. There is a fracture from the dorsal to the anterior edge in right lateral view. It coincides with bite mark #1 (= dorsal-most bite mark).

Discussion: Based on the morphology, the vertebra (SMP VP-2407) is identified as a mid-caudal vertebra of a theropod, somewhere between caudal vertebrae 10 -15. While caudal vertebrae of large theropods such as tyrannosauroids tend to be amphiplatyan or amphicoelous distally (Holtz, 2004), SMP VP-2407 is appears to be procoelous, although some of this may be due to weathering of the cranial and caudal surfaces. Part of this may be due to the erosion on the posterior centrum surface, however this is also why the vertebra is identified from a region proximal to the distal caudal vertebrae. Sutures are present on the remnants of the neural arch. This is interpreted as a sub-adult feature because the neural arch had not ossified with the vertebral centrum. It is similar to caudal vertebrae identified as *Tyrannosaurus rex* (e.g., Brochu, 2003) and other tyrannosaurids (e.g., Holtz, 2004), and so is identified as a large theropod, probably a sub-adult tyrannosaurid.

Of note are the multiple bite marks on both sides of the vertebra (SMP VP-2407). Both sides exhibit five bite marks; however, the size of the marks and spacing between the marks is distinct between both sides. Bite mark #1 on the left side (Fig. 3A-C) is more ovoid and robust, suggest a puncture mark, whereas bite mark #2 is similar but has a tapered end, suggesting a puncture and drag event. Spacing between the bite marks on the left side is inconsistent, with some being wider, while others are conspicuously close to each other. All five traces represent puncture marks, with no scoring marks, or “bite-and-drag” marks present.

On the right side, all the bite marks represent blade-like teeth, and are more consistently spaced. Unlike the left side, two marks (#2 and #3) on the right side represent “bite-and-drag” events. On the right side, bite mark #1 is associated with an oblique fracture, which may represent post-mortem damage. Bite marks #4 and #5 are small puncture marks.

Material: SMP VP-3375, indeterminate theropod posterior dorsal vertebra (Fig. 4).

Locality: SMP loc. 401 (Bob’s Bloody Bluff [North Side]), Ah-shi-sle-pah WSA.

Formation/Member: Kirtland Formation (Hunter Wash Formation).

Description: SMP VP-3375 represents a posterior dorsal vertebra of a questionable medium-sized theropod (Fig. 4). The centrum has a maximum length (craniocaudally) of 5.6 cm and a maximum height (measured along the midline at the cranial end) of 7.1 cm. The preserved portion of the vertebra has a maximum height (measured from the ventral base to the top of the preserved portion of the neural spine) of 30.7 cm and a width (measured midway through the centrum) of 5.6 cm. The dimensions (height to the base of the neural canal by maximum width) of the anterior surface of the centrum are 7.0 cm by 6.1 cm, while those of the posterior surface are 6.7 cm by 6.0 cm. The neural canal is preserved and has dimensions of 2.4 cm (height) by 2.5 cm (width). The neural spine is incomplete, missing its distal-most (or dorsal-most) portion and the posterior (or caudal) edge. The neural spine has a maximum preserved height (measured from the distal edge of the neural canal to the preserved tip) of 20.1 cm and a maximum length (anteroposteriorly) of 3.7 cm. Portions of the anterior surface of the centrum have been eroded away, and the entire posterior-surface of the centrum is heavily weathered (Stage 5 of Behrensmeyer, 1978). The neural spine exhibits a natural anterior curve as it projects dorsally, and does not show any evidence of the curve being due to a pathology or distortion. Preserved portions include the prezygapophyses, the right diapophysis and part of the left, the centrodiapophyseal laminae, the right parapophyseal centrodiapophyseal fossa, and part of the right postzygapophysis.

Bite marks are present on both the left and right sides of the vertebral centrum. The left side has at least four bite marks (Fig. 4A-C, with potentially two other small marks. The main four marks are puncture marks, with slight evidence of “bite-and-drag”. Two other smaller marks are also present toward the anterior of the vertebra and are believed to represent smaller bite marks. Of the four main bite marks on the left side, the largest measures 0.9 cm in total length, and the smallest measures 0.2 cm. Spacing between the traces (from dorsal to ventral) is 0.6 cm, 0.7 cm, and 0.4 cm with respect to the main four

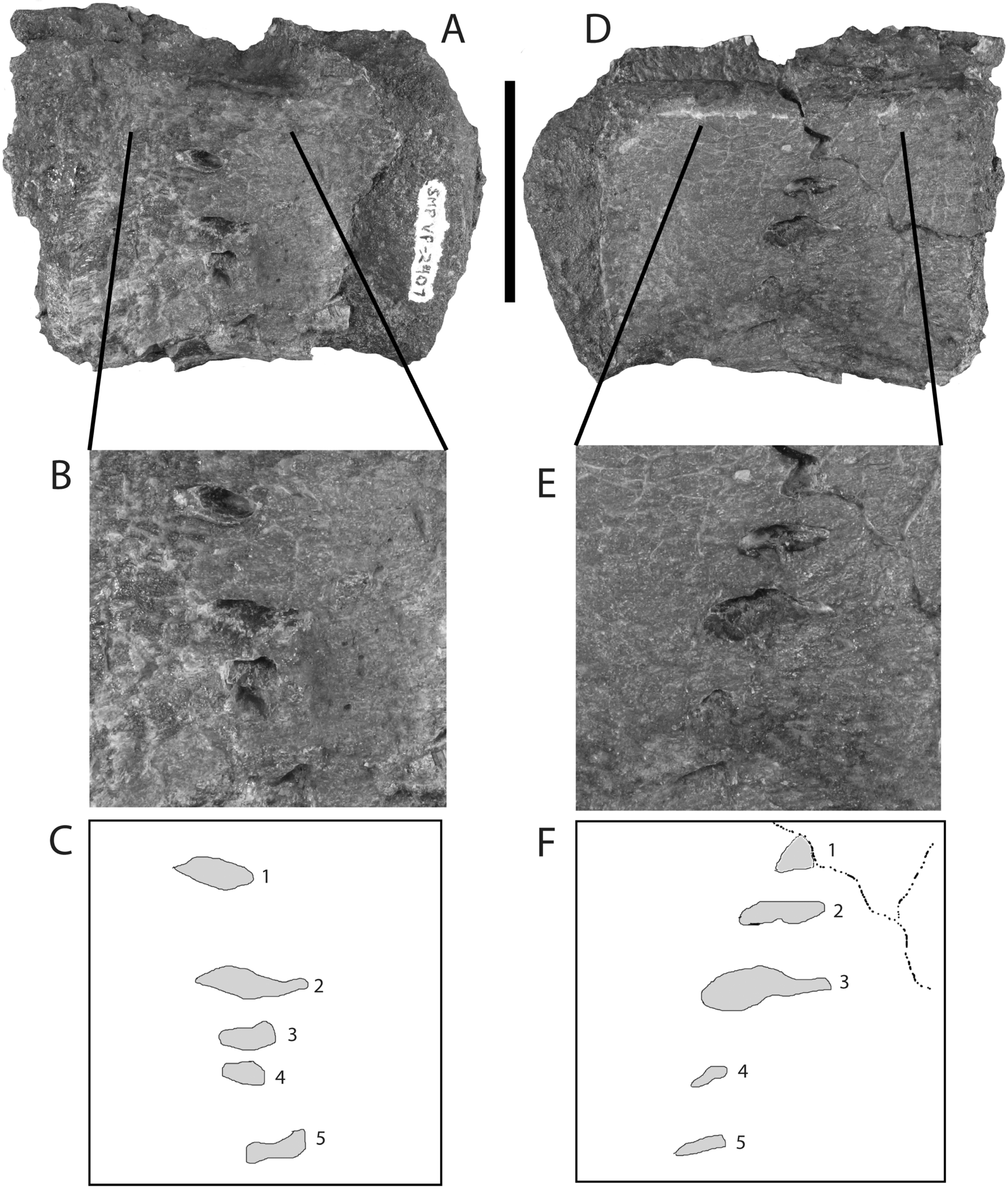

FIGURE 3. Theropoda indeterminate, SMP VP-2407, sub-adult caudal vertebra (?C1-?C15) in: **A**, left lateral view; **B**, magnified portion showing traces of bite marks; **C**, illustration of same, highlighting the bite marks (in grey); **D**, right lateral view; **E**, magnified portion showing the bite marks; and **F**, illustration of same highlighting the bite marks (in grey). Bar scale = 5 cm.

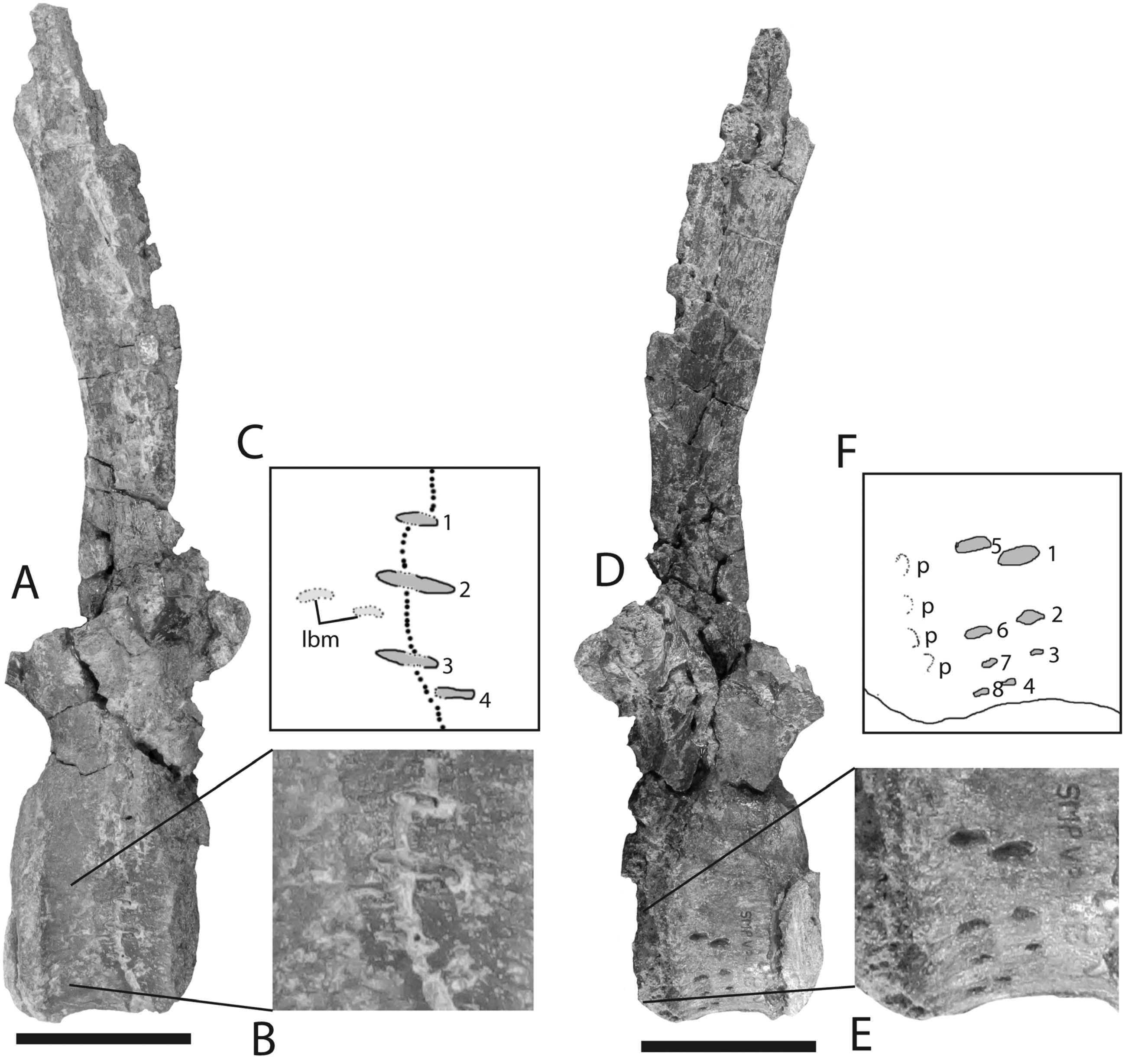

FIGURE 4. Theropoda indeterminate, SMP VP-3375, adult posterior dorsal vertebra in: **A**, left lateral view; **B**, magnified portion showing traces of bite marks; **C**, illustration of same, highlighting the bite marks (in grey); **D**, right lateral view; **E**, magnified portion showing the bite marks in right lateral view; and **F**, illustration of same highlighting the bite marks (in grey). **Abbreviation**: **lbm**, lesser bite mark; **p**, possible bite mark. Bar scales = 5 cm.

bite marks on the left side. There is also a fracture running through the bite marks on the left side. This fracture may have been caused by the initial feeding behavior.

The right side has eight total traces of bite marks in two distinct rows. The largest bite mark on the right side is 0.5 cm in total length, while the smallest is 0.1 cm. The anterior-most row has three distinct bite marks, with a fourth offset somewhat posteriorly. Spacing between the traces of the anterior-most row on the right side are 1.0 cm, 0.6 cm, and 0.7 cm. The second row has four distinct bite marks whose morphology closely adheres to those in the anterior-most row. Spacing between the traces of the second row are 1.2 cm, 0.6 cm, and 0.8 cm, respectively. As noted above, the corresponding bite marks present between the two rows are quite similar and they may represent the same subset of teeth. The broken posterior surface of the right side exhibits at least three features that may be parts of additional bite marks. These bite marks may have fractured the posterior surface and broken off portions of the posterior surface of the centrum.

Discussion: Based on the morphology, including the shape of the centrum, orientation of the diapophyses, and the height and shape of the neural spine, the vertebra (SMP VP-3375) is identified as a posterior dorsal vertebra of a medium-sized theropod dinosaur. SMP VP-3375 was previously believed to be from a hadrosaur, in part due to the relatively large size of the neural spine (see above). However, a recent study did report on a non-spinosaurid theropod (the ornithomimid *Deinocheirus mirificus*) with tall, or relatively tall, neural spines on dorsal vertebrae (Lee et al., 2014). The natural anterior curve of the neural spine also suggests that SMP VP-3375 is from a theropod and not a hadrosaur. Indeed, based on previous taxa from the Late Cretaceous San Juan Basin, SMP VP-3375 most likely represents an ornithomimid or ornithomimosaur, although it potentially could also represent an indeterminate therizinosaur or oviraptorosaur. No pleurocoels are present, making the potential of it being the latter identificationj highly unlikely. This identification is more uncertain due to the large amount of weathering, especially on the posterior surface of the specimen. However, due to the fact that the neural spine is fused to the centrum, SMP VP-3375 is believed to represent an adult, medium-sized theropod.

Multiple traces of bite marks are present on both lateral sides of the vertebra (SMP VP-3375). The left side bears at least four, and possibly six, bite marks. As noted above, the fracture that runs perpendicular through the four main bite marks may have been caused by the feeding behavior of a theropod. The two rows of bite marks on the right side of the centrum can be interpreted in multiple ways. In one instance, the bite marks would have been created by the anterior teeth and would represent two biting events. In a second instance, they may show at least four biting events, with the teeth representing more distal teeth in the side of the mouth. The tooth marks on the right side are not very long, but are relatively deep, implying strong bites from relatively thin, pointed teeth. The questionable third row of bite marks on the posterior portion of the right side of the centrum may have caused a fracture, or may have aided in the posterior portion of the centrum breaking off and/or being more easily eroded. All bite marks appear to be puncture marks, with no evidence of scoring or "bite-and-drag" marks on the right side.

PREDATION OR SCAVENGING?

All three vertebrae (SMP VP-2206, VP-2407, and VP-3375) exhibit puncture marks, while SMP VP-2407 exhibits the most clear "bite-and-drag" marks. "Bite-and-drag" marks are also present, albeit less distinctly, in SMP VP-2206 and VP-3375, with each bearing one example. Each vertebra exhibits bite marks on both the left and right sides. These marks are similar to those reported on the limb bone of a hadrosaurid by Rivera et al. (2013, fig. 1). It is of note, as mentioned above, that one of the bite marks on SMP VP-2206 may potentially show signs of healing. However the rounded rim of that trace does not show trabeculae, exostosis, or texturing of a healed injury, and may instead be evidence of weathering or breakage as well. The orientation of the long axis of the bite marks is always parallel to the long axis of the centrum (longitudinal). This implies that the long axis of the head of the theropod was also parallel to the long axis of the centrum. This means that the bite came from either anterior or posterior to the centrum, and the position of the biting theropod can be derived from the direction of the "bite-and-drag" marks. In SMP VP-2206 and VP-3375, the direction of the bite comes from the posterior, where the theropod would have been standing. However, in SMP VP-2407, the bite comes from the anterior direction. Indeed, this direction and bite mark orientation is known from other reported specimens, including a bite mark from a tyrannosaurid that had healed on the caudal vertebrae of a hadrosaurid (see DePalma et al., 2013).

In the case of these vertebrae, dismemberment must have occurred for the orientation of the theropod's head to be correct to make the observed bite marks. For SMP VP-2206, this would mean a large portion of the trunk must have been removed or not present so that the theropod could get at a dorsal vertebra from the posterior end. Similarly, for SMP VP-3375, the rear portion, including the tail and sacrum/pelvic region, must have been removed to be able to get at a posterior dorsal vertebra from the posterior (or caudal) direction. Conversely, since SMP VP-2407 represents a caudal vertebra and is bitten from the anterior (or cranial) direction, the tail, or a portion thereof, must have been removed or dismembered. If the tail had been removed, the biting theropod could have worked posteriorly from the anterior portions of the tail, where more significant amounts of flesh would be found.

The humerus (NMMNH P-70319) shows obvious signs of feeding along the prominent ridge on the caudal side of the deltopectoral crest. It is unknown as to whether these marks were caused by a primary predator attack or if they are result of subsequent feeding by a theropod, a different predator, or a scavenger. That notwithstanding, the evidence on the bone still suggests that at some point in time it was fed upon by a predator. It is unclear if the arm was dismembered at the time of feeding or was still attached to the body of the hadrosaurine. However, the specimen was found as an isolated element, which is consistent with dismemberment, as are most vertebrate fossils from the Kirtland Formation. The accessibility of flesh on the humerus may have made it an important feeding region. Moreover, the humerus can be a key target area for any predator. Indeed, previous studies have shown bite marks on hadrosaurid humeri as well (Hone and Watabe, 2010). This suggests the possibility that the marks on the humerus may have been caused by predation rather than subsequent scavenging. It is also noted that marks similar to those preserved on SMP VP-3375 have been found on specimens previously reported to have been made by crocodilians (e.g., Njau and Blumenschine, 2006, fig. 6). However crocodilian bite marks tend to be rounded or sub-rounded (e.g., Njau and Blumenschine, 2006; Rivera-Sylva et al., 2009; Noto et al., 2012; Boyd et al., 2013; Botfalvai et al., 2014; Drumheller and Brochu, 2014), and as such the marks present agree more with theropod rather than crocodilian bite marks.

Predators will commonly consume the most easily accessible and desirable portions of flesh immediately after a kill. Although regions such as around the pelvis, thighs, and proximal tail would offer better areas for predators to get large amounts of meat and flesh, the humerus and upper forelimb area could also be a key area. However the vertebral column, and the ribs immediately in the vicinity, do not offer the best, or the highest quality of, flesh possible. The vertebral regions of a prey animal would only be consumed or dismembered after the more desirable portions are presumably gone. Although it is of note that the vertebral column may have been dismembered to allow for portions of the carcass to be more easily moved. Indeed, this is what is thought happened with SMP VP-2407 (discussed above). Based on the bite marks on the vertebrae, and the fact that some of the vertebrae seem to show multiple biting events, it seems clear that these bite marks provide evidence of scavenging behavior, unlike the humerus. Indeed, it seems evident that the prey animals' vertebrae must have been dismembered during the feeding process by theropod dinosaurs.

The tooth marks are different shapes and sizes and appear to represent different theropods, although these differences could be taxonomic or ontogenetic. Moreover, based on the overall size and dimensions of the bite marks, it seems probable that the perpetrators were large theropods of different ontogenetic stages and/or species. Based on the known theropods from the Campanian of the San Juan Basin, New Mexico (e.g., Carr and Williamson, 2010), we conclude that all three vertebrae were probably scavenged by tyrannosauroids of different ages. While it is noted that SMP VP-2407 and NMMNH P-70319 are both hadrosaurids which, not surprisingly, are considered a common prey animal for large theropods; SMP VP-2206 and VP-3375 on the other hand, point to theropods as potential food sources for other theropods, be it from scavenging or predation (e.g., Rogers et al., 2003). While both individuals would have previously died and beenscavenged, it is still noteworthy that these dead theropods were scavenged by other large theropods. SMP VP-2407 is believed to represent a large theropod that was dismembered and scavenged by another large theropod. SMP VP-3375, on the other hand, was a medium-sized theropod that was then scavenged by another theropod.

TAPHONOMIC AND DEPOSITIONAL IMPLICATIONS

SMP VP-2206 and VP-3375 have interesting implications for taphonomy and deposition. SMP VP-2206 exhibits a narrow furrow that is believed to be from an insect or bacteria. Indeed, similar furrows present on fossil vertebrate remains have previously been attributed to insect damage, mainly believed to be feeding damage (e.g., Kaiser, 2000; Fejfar and Kaiser, 2005; Bader et al., 2009). This suggests that the bone sat on the surface for a while before complete burial, facilitating scavenging. SMP VP-3375, on the other hand, does not exhibit insect or bacterial damage, but does exhibit pronounced weathering. This is evident on the posterior surface, including the centrum and neural spine. It seems the bone would have been partially covered with its anterior surface buried and its posterior surface exposed. This could have led to more extreme weathering on the posterior surface, and may have led to the scavenging evident on the lateral surfaces of the bone. SMP VP-2407 does not exhibit the taphonomic features of the two vertebrae discussed above. However, in addition to the unfused neural arch leading to the lack of a neural spine with the specimen, the vertebra is also slightly deformed asymmetrically, with the dorsal portion of the left side shifted slightly to the right.

NMMNH P-70319, while well preserved, exhibits weathering coupled with pitting primarily on the distal end of the humerus (roughly Stage 3 of Behrensmeyer, 1978). This pitting and weathering is what is expected from the weathering of non-fossilized bone on the surface (see Behrensmeyer, 1978), and as such does not represent modern weathering of the fossilized specimens. This weathering and pitting suggests surface exposure prior to burial (see Behrensmeyer, 1978) rather than potentially weathering of fossil specimens after exhumation. Compression fractures noted above were probably the result of sediment compaction after burial.

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REFERENCES

Bader, K.S., Hasiotis, S.T., and Martin, L.D., 2009, Application of forensic science techniques to trace fossils on dinosaur bones from a quarry in the Upper Jurassic Morrison Formation, northeastern Wyoming: Palaios, v. 24, p. 140–158.

Behrensmeyer, A.K., 1978, Taphonomic and ecologic information from bone weathering: Paleobiology, v. 4, p. 150–162.

Botfalvai, G., Prondvai, E., and Ősi, A., 2014, Inferred bite marks on a Late Cretaceous (Santonian) bothremydid turtle and a hylaeochampsid crocodilian from Hungary: Cretaceous Research, v. 50, p. 304–317.

Boyd, C.A., Drumheller, S.K., and Gates, T.A., 2013, Crocodyliform feeding traces on juvenile ornithischian dinosaurs from the Upper Cretaceous (Campanian) Kaiparowits Formation, Utah: PLoS ONE, v. 8, e57605, 8 p.

Brochu, C.A., 2003, Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull: Journal of Vertebrate Paleontology, Memoir 7, 138 p.

Brown, B., 1910, The Cretaceous Ojo Alamo beds of New Mexico with description of the new dinosaur genus *Kritosaurus*: Bulletin of the American Museum of Natural History, v. 28, p. 267–274.

Carpenter, K., 1998, Evidence of predatory behavior by carnivorous dinosaurs: GAIA, v. 15, p. 135–144.

Carpenter, K., Sanders, F., McWhinney, L.A., and Wood, L., 2005, Evidence for Predator-Prey Relationships; *in* Carpenter, K. ed., The Carnivorous Dinosaurs. Bloomington, Indiana University Press, p. 325–350.

Carr, T.D., and Williamson, T.E., 2010, *Bistahieversor sealeyi*, gen. et sp. Nov., a new tyraanosauroid from New Mexico and the origin of deep snouts in Tyrannosauroidea: Journal of Vertebrate Paleontology, v. 30, p. 1-16.

Chure, D.J., Fiorillo, A.R., and Jacobsen, A., 2000, Prey bone utilization by predatory dinosaurs in the Late Jurassic of North America, with comments on prey bone use by dinosaurs throughout the Mesozoic: Gaia, v. 15, p. 227–232.

DePalma, II, R.A., Burnham, D.A., Martin, L.D., Rothschild, B.M., and Larson, P.L., Physical evidence of predatory behavior in *Tyrannosaurus rex*: Proceedings of the National Academy of Sciences of the United States of America, v. 110, p. 12560–12564.

Drumheller, S.K., and Brochu, C.A., 2014, A diagnosis of *Alligator mississippiensis* bite marks with comparisons to existing crocodilian datasets: Ichnos, v. 21, p. 131–146.

Erickson, G.M., and Olson, K.H., 1996, Bite marks attributable to *Tyrannosaurus rex*: preliminary description and implications: Journal of Vertebrate Paleontology, v. 16, p. 175–178.

Erickson, G.M., Van Kirk, S.D., Su, J., Levenston, M.E., Caler, W.E., and Carter, D.R., 1996, Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones: Nature, v. 382, p. 706–708.

Fejfar, O., and Kaiser, T.M., 2005, Insect bone-modification and paleoecology of Oligocene mammal-bearing sites in the Doupov Mountains, northwestern Bohemia: Palaeontologia Electronica, v. 8, 8A, 11 p.

Fiorillo, A.R., 1991, Prey bone utilization by predatory dinosaurs: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 88, p. 157–166.

Fowler, D.W., and Sullivan, R.M., 2006, Ceratopsid pelvis with tooth marks from the Upper Cretaceous Kirtland Formation, New Mexico: Evidence of late Campanian tyrannosaurid feeding behavior: New Mexico Museum of Natural History and Science, Bulletin 35, p. 127–130.

Holtz, T.R., Jr., 2004, Tyrannosauroidea; p. 111–136 *in* Weishampel, D.B., Dodson, P., and Osmólska, H., eds., The Dinosauria: University of California Press, Berkeley.

Holtz, T.R., Jr., 2008, A critical reappraisal of the obligate scavenging hypothesis for *Tyrannosaurus rex* and other tyrant dinosaurs; p. 371–396 *in* Larson, P. and Carpenter, K., eds., *Tyrannosaurus rex*, the Tyrant King. Indiana University Press, Bloomington.

Hone, D.W.E., and Rauhut, O.W.M., 2010, Feeding behaviour and bone utilization by theropod dinosaurs: Lethaia, v. 43, p. 232–244.Hone, D.W.E., and Watabe, M., 2010, New information on scavenging and selective feeding behavior of tyrannosaurids: Acta Palaeontologica Polonica, v. 55, p. 627–634.

Horner, J.R., Weishampel, D.B., and Forster, C.A., 2004, Hadrosauridae; p. 438–463 *in* Weishampel, D.B., Dodson, P., and Osmólska, H., eds., The Dinosauria: University of California Press, Berkeley.

Hunt, A.P., and Lucas, S.G., 2015, Vertebrate trace fossils from New Mexico and their significance: New Mexico Museum of Natural History and Science, Bulletin, in press.

Jasinski, S.E., 2015, A new dromaeosaurid (Theropoda: Dromaeosauridae) from the Late Cretaceous of New Mexico: New Mexico Museum of Natural History and Science, Bulletin, in press.

Jasinski, S.E., Sullivan, R.M., and Lucas, S.G., 2011, Taxonomic composition of the Alamo Wash local fauna from the Upper Cretaceous Ojo Alamo Formation (Naashoibito Member) San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 53, p. 216–271.

Kaiser, T.M., 2000, Proposed fossil insect modification to fossil mammalian bone from Plio-Pleistocene hominid-bearing deposits of Laetoli (northern Tanzania): Annals of the Entomological Society of America, v. 93, p. 693–700.

Lucas, S.G., 1981, Dinosaur communities of the San Juan Basin: A case for lateral variations in the composition of Late Cretaceous dinosaur communities; in Lucas, S.G., Rigby, J.K., Jr. and Kues, B.S., eds., Advances in San Juan Basin Paleontology; Albuquerque, University of New Mexico Press, p. 337–393.

Lucas, S.G., 1993, Dinosaurs of New Mexico: New Mexico Academy of Science, v. 32, 130 p.

Lucas, S.G., Heckert, A.B., and Sullivan, R.M., 2000, Cretaceous dinosaurs of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 83–90.

Lucas, S.G., Mateer, N.J., Hunt, A.P., and O'Neill, F.M., 1987, Dinosaurs, the age of the Fruitland and Kirtland Formations, and the Cretaceous-Tertiary boundary in the San Juan Basin, New Mexico; in Fassett, J.E. and Rigby, J.K., Jr., eds., The Cretaceous-Tertiary Boundary in the San Juan and Raton Basins, New Mexico and Colorado. Geological Society of America Special Paper, v. 209, p. 35–50.

Njau, J.K., and Blumenschine, R.J., 2006, A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania: Journal of Human Evolution, v. 50, p. 142–162.

Noto, C.R., Main, D.J., and Drumheller, S.K., 2012, Feeding traces and paleobiology of a Cretaceous (Cenomanian) crocodyliform: example from the Woodbine Formation of Texas: Palaios, v. 27, p. 105–115.

Peterson, J.E., Henderson, M.D., Scherer, R.P., and Vittore, C.P., 2009, Face biting on a juvenile tyrannosaurid and behavioral implications: PALAIOS, v. 24, p. 780-784.

Rivera-Sylva, H.E., Frey, E., and Guzmán-Gutiérrez, J.R., 2009, Evidence of predation on the vertebra of a hadrosaurid dinosaur from the Upper Cretaceous (Campanian) of Coahuila, Mexico: Carnets de Géologie / Notebooks on Geology, Letter 2009/02, 6 p.

Rivera-Sylva, H.E., Hone, D.A., and Dodson, P., 2013, Bite marks of a large theropod on an [sic] hadrosaur limb bone from Coahuila, Mexico: Boletin de la Sociedad Geológica Mexicana, v. 64, p. 155–159.

Rogers, R.R., Krause, D.W., and Curry Rogers, K., 2003, Cannibalism in the Madagascan dinosaur *Majungatholus atopus*: Nature, v. 422, p. 515–518.

Sullivan, R.M., 2006, *Saurornitholestes robustus*, n. sp. (Theropoda: Dromaeosauridae) from the Upper Cretaceous Kirtland Formation (De-na-zin Member), San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 35, p. 253–256.

Sullivan, R.M., and Lucas, S.G., 2000, First occurrence of *Saurornitholestes* (Theropoda: Dromaeosauridae) from the Upper Cretaceous of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, 105–108.

Sullivan, R.M., and Lucas, S.G., 2003, The Kirtlandian, a new land-vertebrate "age" for the Late Cretaceous of Western North America: New Mexico Geological Society, 54th Field Conference Guidebook, p. 369–377.

Sullivan, R.M., and Lucas, S.G., 2006, The Kirtlandian land-vertebrate "age"—faunal composition, temporal position and biostratigraphic correlation in the nonmarine Upper Cretaceous of western North America: New Mexico Museum of Natural History and Science, Bulletin 35, p. 78–29.

Tanke, D.H., and Currie, P.J., 2000, Head-biting behavior in theropod dinosaurs: paleopathological evidence: Gaia, v. 15, p. 167–184.