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TYRANNOSAUR CANNIBALISM: A CASE OF A TOOTH-TRACED TYRANNOSAURID BONE IN THE LANCE FORMATION (MAASTRICHTIAN), WYOMING

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ABSTRACT: A recently discovered tyrannosaurid metatarsal IV (SWAU HRS13997) from the uppermost Cretaceous (Maastrichtian) Lance Formation is heavily marked with several long grooves on its cortical surface, concentrated on the bone's distal end. At least 10 separate grooves of varying width are present, which we interpret to be scores made by theropod teeth. In addition, the tooth ichnospecies *Knethichnus parallelum* is present at the end of the distal-most groove. *Knethichnus parallelum* is caused by denticles of a serrated tooth dragging along the surface of the bone. Through comparing the groove widths in the *Knethichnus parallelum* to denticle widths on Lance Formation theropod teeth, we conclude that the bite was from a *Tyrannosaurus rex*. The shape, location, and orientation of the scores suggest that they are feeding traces. The osteohistology of SWAU HRS13997 suggests that it came from a young animal, based on evidence that it was still rapidly growing at time of death. The tooth traces on SWAU HRS13997 are strong evidence for tyrannosaurid cannibalism—a large *Tyrannosaurus* feeding on a young *Tyrannosaurus*.

INTRODUCTION

Animal behavior is notoriously difficult to interpret from body fossils (e.g., Benton 2010). The presence of ichnofossils, such as footprints, coprolites, tooth traces, and trampling marks, provides insight into the activities and ecological roles of extinct taxa that would be otherwise unavailable (e.g., Benton 2010; Plotnick 2012). Although trace fossils are very useful in understanding paleobiology, they require interpretation as to what animal created them. This interpretive process is limited by the amount of detail preserved in the fossil trace, which means that it is often not possible to refine the taxonomy of the trace to something that significantly benefits paleoecological interpretations. The more information that can be recovered from the trace fossil, the more confident the interpretation of past behaviors and events.

One behavior that would be expected in some extinct taxa is cannibalism. Cannibalism, defined here as the feeding of one animal upon another member of the same species, has been observed in many extant carnivorous vertebrate taxa (e.g., Polis 1981). Its presence in extant taxa implies that we should find examples of cannibalism in the fossil record. The most famous example of non-avian dinosaur cannibalism for many decades was a specimen of the Triassic theropod *Coelophysis bauri* (AMNH FR 7224), which was thought to show evidence for cannibalistic behavior, but was later shown to be a misinterpretation of the fossil (Nesbitt et al. 2006). Other studies presented convincing evidence for dinosaur cannibalism (Rogers et al. 2003), including examples of cannibalistic behavior among *Tyrannosaurus rex* (Longrich et al. 2010).

In June of 2015, we discovered a large theropod bone fragment (SWAU HRS13997; Fig. 1) attributable to Tyrannosauridae on the surface near a previously unexplored sandstone dinosaur-bearing bonebed in the Maastrichtian Lance Formation of the Powder River Basin in eastern Wyoming. Clustered on one end of the bone were a series of subparallel scratches perpendicular to the long axis of the bone. We interpret these scratches to be tooth scores from a tyrannosaurid dinosaur. We studied these scores to discern whether this represented an example of tyrannosaurid cannibalism or some other feeding or non-feeding behavior, and to glean insights into tyrannosaurid behavior.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, New York; FMNH, Field Museum of Natural History, Chicago, Illinois; IGM, Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, Mexico; LACM, Los Angeles County Museum of Natural History, Los Angeles, California; MOR, Museum of the Rockies, Bozeman, Montana, USA; SWAU, Southwestern Adventist University, Keene, Texas, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen 1842
Saurischia Seeley 1887
Theropoda Marsh 1881
Tyrannosauroidea Walker 1964
Tyrannosauridae Osborn 1906
Tyrannosaurus Osborn 1905
Tyrannosaurus rex Osborn 1905

Material.—SWAU HRS13997, a partial right metatarsal IV.

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FIG. 1.—A *Tyrannosaurus rex* metatarsal IV (SWAU HRS13997) in four views. Scale bar = 100 mm.

Locality.—Niobrara County, eastern Wyoming, USA.

Diagnosis.—The hollow core of SWAU HRS13997 is evidence that it came from a theropod, and the large size of the bone and thickness of the bone walls coupled with its presence in the Lance Formation suggests that it came from a tyrannosaurid. We have identified SWAU HRS13997 to be a partial right metatarsal IV as evidenced by the flattened region on the medial surface that is the contacting surface with the distinctive metatarsal III of tyrannosaurids, which narrows to a point medially (Holtz 2004). Since the only tyrannosaurids currently recognized in the Lance Formation are *Tyrannosaurus rex* and possibly *Nanotyrannus lancensis*, it very likely belongs to one of these two. Because the individual was at the purported size of a mature *Nanotyrannus lancensis*, yet immature and still rapidly growing, we conclude that the bone is from a *Tyrannosaurus rex* (see histological description in Results).

Description.—Both the proximal and distal ends of SWAU HRS13997 are broken, resulting in a length of 280 mm for what remains of the element. In addition to the fractures at the distal and proximal ends, a section of the shaft is missing, which exposes the hollow core of the bone (Fig. 1, online Supplemental File fig. 1).

METHODS

After excavation, SWAU HRS13997 was prepared and photographed with a Canon Mark II 5D camera and an electronically coupled turntable. This allows for a 3DVR image of the bone to be created, which is available for viewing at http://fossil.swau.edu. The scratches on the bone were carefully observed and photographed using a Nikon SMZ 1500 with a Nikon DS-Fi1 Digital Sight camera, and they were measured using the Nikon NIS-Element Basic Research v. 4.30.02. The widths of the striations on the *Knethichnus parallelum* were measured and compared to denticle widths on theropod teeth obtained from nearby Lance Formation quarries (see online Supplementary File for the list of specimens measured). We compared SWAU HRS13997 to tyrannosaurid material from the LACM for identification purposes, specifically LACM 23845, a specimen from Montana originally considered to be from *Albertosaurus* cf. *Albertosaurus* (=*Nanotyrannus*) *lancensis* (Molnar 1980), then described as a new species (*Albertosaurus megagracilis*, (Paul 1988)), which was later placed in a new genus *Dinotyrannus* (Olshevsky 1995), but is now considered to be a "subadult" *Tyrannosaurus rex* (Carr and Williamson 2004). We also consulted figured tyrannosaurid material in the literature (e.g., Brochu 2003).

We prepared a cross-sectional thin section from the middle of SWAU HRS13997 to study the histology of the bone and determine the animal's age at the time of its death. Because of the condition of the bone (Fig. 1), we choose to sample from a region with a complete record of the cortex and as close to the mid-diaphysis as possible. Although metatarsals are not commonly sampled, comparative histological sampling among different elements of the same individual of *Alligator mississippiensis* has shown that the mid-diaphysis of the metatarsals preserve a large amount of skeletochronological information (Garcia 2011), and so we are confident that the sectioned tyrannosaurid metatarsal records an adequate record of growth. The proximal-most 40 mm of the bone was embedded in AeroMarine (www.aeromarineproducts.com) epoxy (#300) and hardener (#21) following the methods outlined by Lamm (2013). The embedded sample was cut using a Covington 5047HG rock saw and ground with Covington diamond lapidary discs (NB1210, NB1220, NB1227, NB1232, and RB1260) using a series of diamond embedded wheels ranging from 100–600 grit. Once the embedded sample was

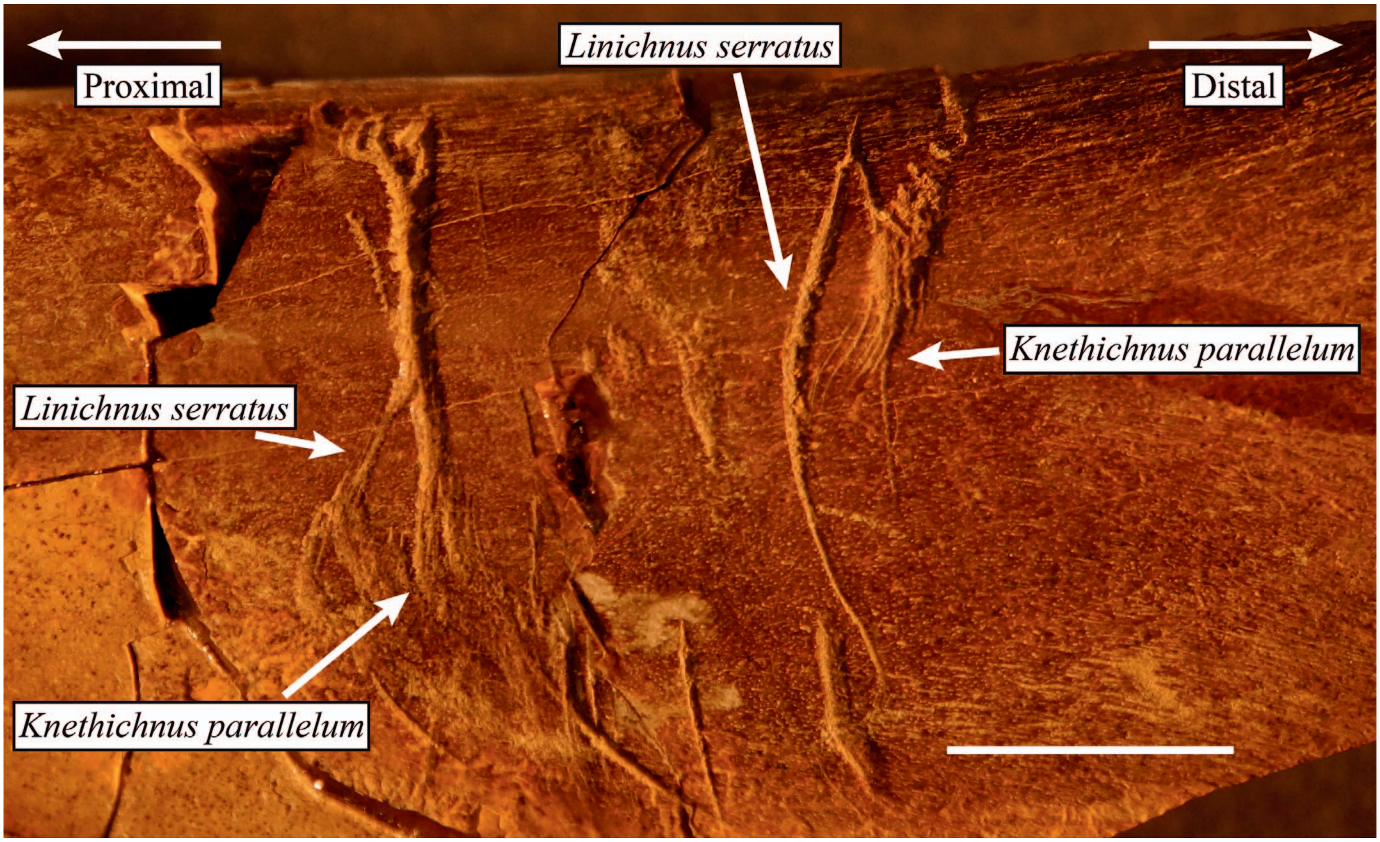

FIG. 2.—Tooth traces on SWAU HRS13997. The two sets of *Knethichnus paralleum* and *Linichnus serratus* are indicated, with the more prominent pair on the right. Scale bar = 20 mm.

polished and dried, the section was affixed to the frosted side of a 3″×4″ glass slide using two-ton epoxy (Devcon GLU-735.90), and allowed to cure overnight. The sample + slide were cut on a rock saw so that the glass slide retained a 1-inch section of embedded bone. The glass slide was then ground using a series of progressively finer grit wheels ending when the sample was evenly transparent (see Lamm (2013) for more detail). The sample was finally hand-ground with 600 grit tungsten carbide powder until the desired opacity was obtained (~ 70–100 microns thick). The thin section was viewed with a Nikon Eclipse LV100ND transmitted and reflected light microscope and imaged with a Nikon DS-Fi2 camera and Digital sight DS-U3 interface. High resolution images of the entire slide were captured with this microscope and camera using a Prior ProScan III automated microscope state and digitally assembled using Nikon NIS-Element Basic Research v. 4.40.00 (Build 1084). Images were captured in four light regimes: plane-polarized light, cross-polarized light, cross-polarized light with a gypsum plate (125 nm), and reflected light. Large high-resolution whole-slide images have been uploaded onto the online repository Morphobank (http://www.morphobank.org/, Project Number 2584).

RESULTS

SWAU HRS13997 shows no signs of weathering, although it does show stage 1 abrasion in the form of slight rounding to broken edges of the element, following the definition from Ryan et al. (2001). From comparison with a similar-sized *Tyrannosaurus* metatarsal on display at the Los Angeles County Museum (LACM 23845) we interpret the original length of SWAU HRS13997 to be ~ 450 mm.

Tooth Traces

The scratches on the proximal end of SWAU HRS13997 match descriptions of tooth scores found in the literature, having length to width ratios of greater than 3:1 and U or V-shaped cross sections (Binford 1981; Njau and Blumenschine 2006; Pobiner et al. 2007; Pobiner 2008). Two examples each of the ichnotaxa *Knethichnus parallelum* (Jacobsen and Bromley 2009) and *Linichnus serratus* (Jacobsen and Bromley 2009) occur in close proximity to one another, with one pair more prominent than the other (Figs. 2, 3). The *Knethichnus parallelum* trace is caused by the denticles on a serrated tooth dragging along the surface of a bone (Jacobsen and Bromley 2009) as demonstrated by actualistic experiments on Komodo dragon (*Varanus komodoensis*) feeding behavior (D'Amore and Blumenschine 2012). If the fauna of the formation in question is well known, as is the case with the heavily studied Lance Formation, then the denticle widths on the teeth from the present carnivorous taxa can be compared to the striation widths of the *Knethichnus parallelum* trace to look for a match.

Tooth scores are located on the distal end of the bone. The scores have a U-shaped cross-section and the grooves vary in width from 0.6–6 mm. The proximal-most trace is made of three separate scores which merge into a single score, the deepest trace on the bone. Distal to this trace are the prominent examples of *Linichnus serratus* and *Knethichnus parallelum*. This *Knethichnus parallelum* trace cuts across an earlier score (Fig. 3). Posterior to these traces is an assortment of small, shallow scores. The striation width (SW) of the *Knethichnus parallelum* on SWAU HRS13997 is three striations per 2 mm.

Measurements of average denticle width (DW) on the mesial and distal carinae (MDW and DDW, respectively) on theropod teeth from the Lance Formation (Table 1) compared with the striation width (SW) of three

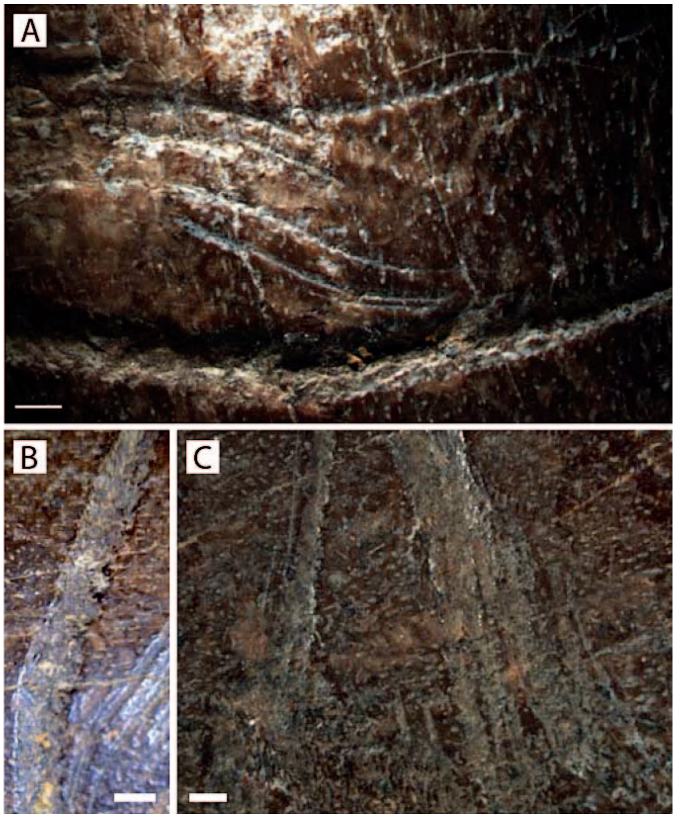

FIG. 3.—Details of *Knethichnus parallelum* and *Linichnus serratus* traces on SWAU HRS13997. **A**) Most prominent *K. parallelum* (center) and *L. serratus* (bottom) examples. **B**) Most prominent *L. serratus* in more detail and a different lighting angle. Small portion of the most prominent *K. parallelum* is also visible in the lower right corner. **C**) Detailed view of the other, less prominent *L. serratus* (left) and *K. parallelum* (right) traces. All scale bars = 1 mm.

striations per 2 mm on the *Knethichnus parallelum* trace on SWAU HRS13997 demonstrate that the DW of most Lance Formation theropods are too small to have created the SW on SWAU HRS13997. In fact, only the DW on teeth of *Tyrannosaurus rex* was large enough to produce the observed SW. As noted by D'Amore and Blumenschine (2012), striation widths on a *Knethichnus parallelum* trace can be equal to or smaller than the denticle width of the biter's tooth, but never larger. Thus, it is not possible that the *Knethichnus parallelum* could have been made by any of the taxa in Table 1 except for *Tyrannosaurus rex*.

Histology

This histological description uses the terminology of Francillon-Vieillot et al. (1990), as described and expanded on by Werning (2013). The histological thin section of SWAU HRS13997 is narrow dorsally, where it forms a rounded apex, with a wide, round ventral surface. The medullary cavity is hollow and the endosteal surface is jagged (Fig. 4A), with no evidence of endosteal lamellae or medullary bone. The inner cortex is composed of highly woven-fibered, unremodeled primary bone (Fig. 4B–4E). Both longitudinal simple vascular canals and primary osteons are common, with primary Haversian cavities present but less common, and most vascular cavities anastomose in no preferred orientation. There is no evidence of secondary remodeling, either by the presence of erosion rooms or secondary osteons. Osteocyte lacunae possess no preferred orientation in this region except for some of the lacunae in the lamellar bone of the primary osteons, which are usually oriented circumferentially around the vascular cavity of the osteon. Although the innermost portion (1.25–2 mm) of the cortex, including the endosteal border, is a deep reddish-brown, the next most external cortical bone is light tan, forming a tan-colored circumferential band 1–2 mm thick; the outermost 2–5 mm of the cortex is also light tan in color (Fig. 4A). This difference in coloration is not correlated with bone tissue or texture, indicating these colored bands are not biological in origin.

Roughly one-fourth to one-half the distance from the endosteal surface to the subperiosteal surface, the vascular style shifts from being predominantly longitudinal canals to circumferential canals, and anastomosing canals become rare in the external-most 2–3 mm of the cortex. The ∼ 2–4 mm closest to the subperiosteal surface possesses patches of more organized parallel-fibered bone which become more common in the external-most region of the cortex, and in these regions osteocyte lacunae are preferentially oriented with the collagen fibers. The dorsal-most region of the cortex is the exception to this description, with highly disorganized woven bone and longitudinal canals predominating to the subperiosteal surface. There are no secondary osteons or erosion rooms in the cortical bone. Although there are several circumferential patterns in the cortical bone, close examination reveals these to be neither lines of arrested growth (LAGs), diagnosed by continuous cement lines (which are apparent in reflected light but absent in this specimen; Fig. 4E, 4I, 4M), or annuli, diagnosed by thin bands of continuous avascular parallel-fibered or lamellar bone (especially apparent in cross-polarized light, but absent in this specimen; Fig. 4C, 4G, 4K). These circumferential patterns are patterns in coloration, or in a few instances represent bands of increased osteocyte density, but are not composed of cement lines or avascular regions of lamellar bone. Therefore, growth marks are absent, and the bone contains anastomosing and interconnected vascular cavities up to the subperiosteal surface. Although the overall vascular density does not noticeably decrease from the medullary cavity to the subperiosteal surface (remaining well to very well vascularized throughout, sensu Werning 2013; Fig. 4), there is a shift in vascular orientation in the cortical bone closer to the subperiosteal surface, so that the inner half of the cortex possesses larger vascular cavities.

DISCUSSION

Although SWAU HRS13997 is fragmentary, we are confident that this bone is a tyrannosaurid metatarsal, specifically, metatarsal IV, because of

TABLE 1.—*Denticle measurements for theropod taxa known from the Lance Formation. Abbreviations: DD/2 mm = distal denticles per two millimeters; DDW = distal denticle width; MD/2 mm = mesial denticles per two millimeters; MDW = mesial denticle width.*

Taxon	# of specimens	AVG MDW (mm)	MD/2 mm	AVG DDW (mm)	DD/2 mm	Literature D/2 mm (MD/DD)
Acheroraptor	15	0.327	6.12	0.334	5.99	
Dakotaraptor	-	-	-	-	-	9.2/6.8 (DePalma et al. 2015)
Nanotyrannus	16	0.333	6.01	0.394	5.08	
Tyrannosaurus	14	0.622	3.22	0.528	3.79	3.7/3.8 (Smith et al. 2005)
Troodon	15	-	-	0.385	5.19	

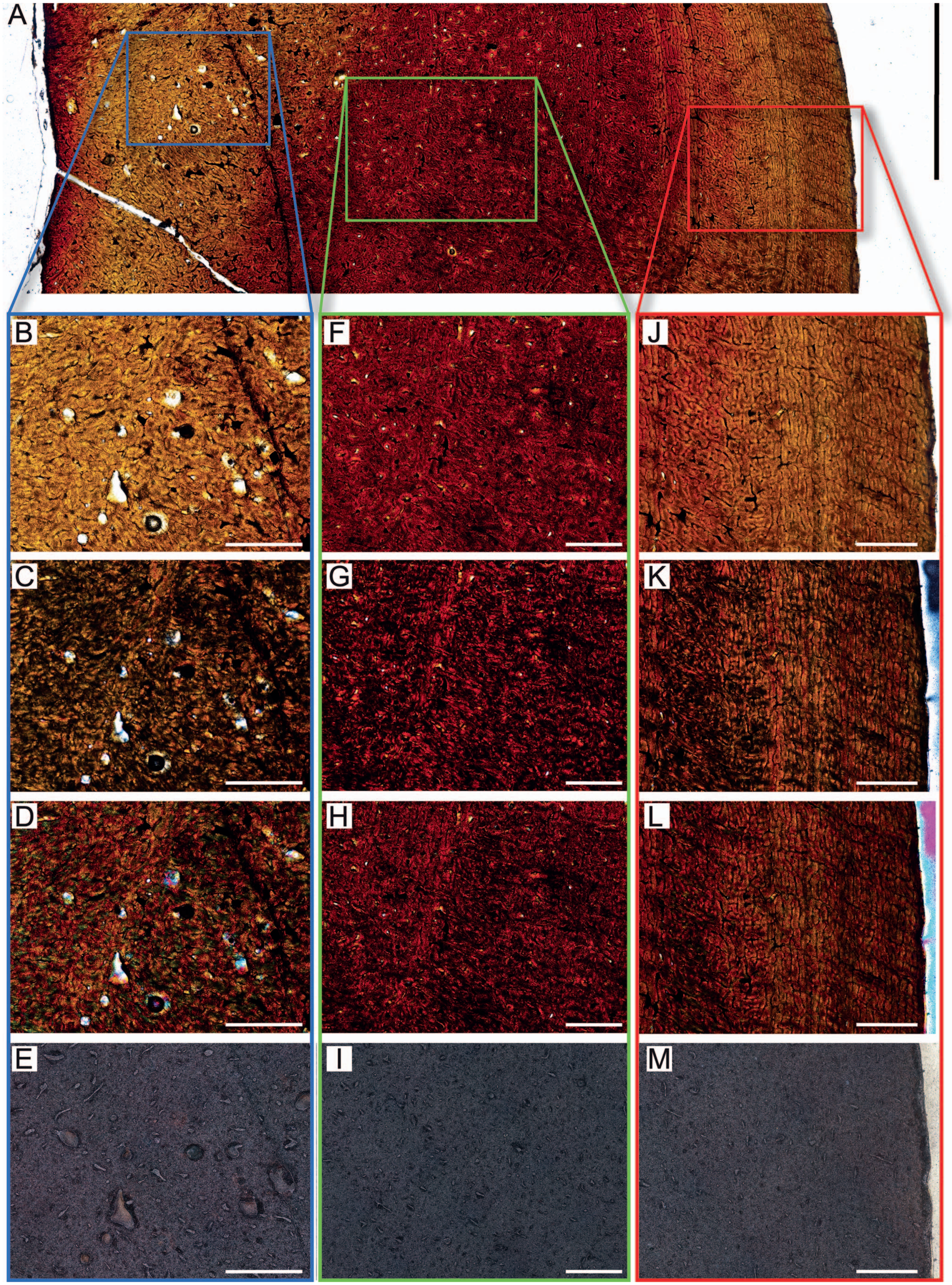
A
B
C
D
E
F
G
H
I
J
K
L
M

FIG. 5.—Comparison between four specimens of tyrannosaurid metatarsals: **A**) *Tyrannosaurus rex* metatarsal IV (SWAU HRS13997). **B**) *Tyrannosaurus rex* metatarsals II-IV (LACM 23845, with IV sculpted). **C**) Tyrannosauridae indet. metatarsal IV (IGM 6130; modified from Peecook (2014, fig. 3). **D**) *Tyrannosaurus rex* metatarsals II-IV (FMNH PR2081; modified from Brochu (2003, figs. 99, 100, 101). SWAU HRS13997 and IGM 6130 are metatarsal IV. All elements are from the right pes except IGM 6130, which is a left element, although the image has been flipped to make it match the others. Note that FMNH PR2081 is shown in a more medial view than the other metatarsal specimens. Scale bar = 100 mm.

similarities between it and the metatarsals of the mounted "subadult" *Tyrannosaurus* on display at the LACM, which is based on material from LACM 23845 (Fig. 5A, 5B, online Supplemental File fig. 1). The fossil specimen LACM 23845 includes an almost complete right foot missing metatarsals I and IV and the phalanges from the first toe (Molnar 1980; Larson 2008). Thus, the metatarsal IV on display is not original but is sculpted based on metatarsals II and III and references to other specimens (P. Fraley, personal communication). Nevertheless, the sculpted metatarsal IV is a relatively accurate model, as evidenced by its similarity to known material from skeletally immature tyrannosaurids, such as "Jane" and IGM 6130 (Peecook et al. 2014) (Fig. 5C). SWAU HRS13997 shares a similar size, diameter, angle of lateral deflection toward the distal end, and the nearly identical flattened medial surfaces for articulation with metatarsal III with the LACM metatarsal IV (online Supplemental File fig. 1), as well as IGM 6130. Initially, we compared SWAU HRS13997 to photographs of bones of the *Tyrannosaurus rex* specimen "Sue" (FMNH PR2081) found in Brochu (2003, Fig. 101). However, after observing bones from various ontogenetic stages of *Tyrannosaurus* at the Natural History Museum of Los Angeles County, we realized that *Tyrannosaurus* metatarsals change in morphology during ontogeny (Fig. 5). The large FMNH PR2081 metatarsals (Fig. 5D) are noticeably less slender, more rugose, and overall more robust than metatarsals from skeletally immature individuals (Fig. 5A–5C), which is consistent with the reasonable assumption that *Tyrannosaurus* feet would have become wider and more robust as the entire animal increased in mass, length, and height through ontogeny. Using an estimated length of 450 mm and the tyrannosaurid long bone regression equations of Currie (2003a), we estimated the femoral length (813 mm) and femoral circumference (309 mm) for this individual. Then, using the Anderson et al. (1985) equation for estimating mass of an organism from femur circumference, we arrived at an estimated mass of 1,000 kg. Inserting this estimated mass into the Erickson et al. (2004) growth curve equation based on mass, we arrived at an estimated age of

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FIG. 4.—Histology of a *Tyrannosaurus rex* metatarsal (SWAU HRS13997) in cross section under different light regimes. **A**) Section of cortical bone from the medullary cavity (left) to the subperiosteal surface (right) under regularly transmitted light. Boxes show where areas of this bone are shown in higher detail under regularly transmitted light (**B**, **F**, **J**), cross-polarized light (**C**, **G**, **K**), cross-polarized light with a waveplate (**D**, **H**, **L**), and reflected light (**E**, **I**, **M**). Scale bar for A = 5 mm, all other scale bars = 1 mm.

thirteen years old. Despite these admittedly tentative estimates, the results are similar to LACM 23845, which was estimated at fourteen years old by Erickson et al. (2004).

We interpret the long grooves on SWAU HRS13997 as tooth scores based on their greater than 3:1 length to width ratios and U-shaped cross sections (Binford 1981; Njau and Blumenschine 2006; Pobiner et al. 2007; Pobiner 2008). The presence of both *Linichnus serratus* and *Knethichnus parallelum* confirm that at least some of these marks were made by serrated teeth. Even though the SW on the *Knethichnus parallelum* most closely matches the DW of *Tyrannosaurus rex* teeth, it is possible that there is another carnivorous varanid or theropod with large denticles in the Lance Formation. Indeed, a large dromaeosaur was recently discovered in the Hell Creek Formation (DePalma et al. 2015), although those authors concluded that *Dakotaraptor* had a higher denticle density than *Tyrannosaurus*, because of its smaller DW (Table 1). Although these marks may have conceivably been made by another unknown contemporaneous carnivorous taxon, the simplest explanation is that these tooth traces were left by *Tyrannosaurus rex.* Since 1965, over 42 *Tyrannosaurus rex* skeletons (5% to 80% complete by bone count) have been collected from western North America (Larson 2008), and *Tyrannosaurus rex* fossils have been found from Alberta to New Mexico (Sampson and Loewen 2005). The plethora of *Tyrannosaurus* fossils that have been found, and the absence of any other large carnivores with appropriately-sized DWs, makes it likely that this trace made by a large theropod is from *Tyrannosaurus* and not some other large, undiscovered taxon.

Because SWAU HRS13997 is from a small Maastrichtian tyrannosaur from western North America, this element could possibly be assigned to the contentious taxon *Nanotyrannus lancensis* (Bakker et al. 1988). Although some researchers consider *Nanotyrannus lancensis* to be a valid species (e.g., Currie 2003b; Larson 2013), other paleontologists view it as a skeletally immature *Tyrannosaurus rex* (e.g., Carr 1999; Holtz 2001, 2004; Carr and Williamson 2004; Brusatte et al. 2010). The osteohistology of SWAU HRS13997 possesses features that are indicative of a young, skeletally immature individual that is still undergoing rapid growth. The high level of vascularization extending to the subperiosteal surface on the outer portion of the histological section suggests that the growth had not ceased in this individual because high vascular density and connectivity is strongly correlated with growth rate (e.g., Montes et al. 2010; Cubo et al. 2012; Fig. 4A, 4J–4M). Further, this vascular structure suggests that growth had not even begun to slow as is expected at the onset of skeletal maturity in tyrannosaurids (e.g., Erickson et al. 2004). Vascular pattern may be somewhat related to relative growth rate (e.g., Amprino 1947; de Ricqlès 1975; Francillon-Vieillot et al. 1990; Castanet et al. 1996, 2000; de Margerie et al. 2002, 2004), but this relationship may be taxon- or species-specific, and the view of a simple relationship between growth and vascular pattern has recently been challenged (Simons and O'Connor 2012; Werning 2013), leaving the relationship between vascular pattern and growth rate unclear. Regardless, the predominant vascular patterns (i.e., longitudinal and circumferential) are consistent with rapid relative growth in those studies that find a correlation between vascular pattern and relative growth rate (e.g., Castanet et al. 2000). Although the precise relationship between Haversian remodeling and maturity varies by clade, the number of secondary osteons present in the cortex of a long bone increases with ontogenetic age (e.g., Horner et al. 1999, 2000; Klein and Sander 2007; Werning 2012), and extensive Haversian remodeling is present in the ribs of the largest known *Tyrannosaurus rex* (FMNH PR 2081; Erickson et al., 2004). However, SWAU HRS13997 possesses no secondary osteons (Fig. 4), even though as a smaller, weight-bearing element it is more likely to experience secondary remodeling, and to experience it earlier in ontogeny (Padian et al. 2016). Therefore, the complete lack of secondary remodeling also supports SWAU HRS13997 as a rapidly growing, immature individual that has not approached full size. We are confident that this element does not belong to an individual of *Nanotyrannus*, but is most likely the metatarsal of an immature *Tyrannosaurus*.

Tyrannosaurid tooth scores, like those on SWAU HRS13997, have been found on other fossils (e.g., Jacobsen 1998, 2001; Hone and Watabe 2010), as have punctures and furrows (Erickson and Olson 1996). Given the robust jaws and teeth of tyrannosaurids, one might expect tyrannosaurid tooth traces on bones to be deeper than seen on SWAU HRS13997. Indeed, it has been demonstrated, both through functional morphology studies and direct fossil evidence, that tyrannosaurids could bite deeply into bones (e.g., Erickson and Olson 1996; Erickson et al. 1996; Meers 2002; Bates and Falkingham 2012 as predicted by Bakker et al. 1988), and tyrannosaurids probably had the strongest skulls (i.e., most resistant to bending) of any theropod (Henderson 2002). Additionally, tyrannosaurid teeth occasionally show irregular spalled surfaces which are caused by tooth contact with food, probably bones, although it is difficult to determine whether this contact was intentional or not (Schubert and Ungar 2005).

Further support for powerful bites in tyrannosaurids is found in their very strong teeth, wider and longer than most other theropod dinosaurs (Farlow et al. 1991). Skeletally immature tyrannosaurids possess serrated and labiolingually compressed (ziphodont) teeth as do other theropods (although with crowns still thicker labiolingually than those of similarly sized theropods (Holtz 2004)), but skeletally mature tyrannosaurids have incrassate maxillary and dentary teeth (Holtz 2001, 2004, 2008) that are considerably thicker labiolingually such that the labiolingual width is sometimes even thicker than the mesiodistal length (Bakker et al. 1988; Holtz 2004).

Nevertheless, there are shallow bite traces attributed to tyrannosaurids, such as scrape feeding on a *Saurolophus* humerus (Hone and Watabe 2010). The ability to selectively feed is reflected in the teeth of tyrannosaurids, which have more obvious heterodonty than other large carnivorous theropods (Smith 2005) in that their premaxillary teeth are considerably smaller than their maxillary (or lateral) teeth (Holtz 2004) and possess D-shaped cross-sections, as does *Eotyrannus* (Hutt et al. 2001). Although the premaxillary teeth of tyrannosauroids differ significantly in morphology from the rest of their dentition, there does not appear to be any significant difference in the average denticle densities on either the mesial or distal carinae when compared to those of the dentary or maxillary teeth (Smith et al. 2005). The premaxillary teeth of tyrannosaurids were more closely spaced than the maxillary or dentary teeth, and they were probably used in nipping and scraping flesh off of bones (Erickson and Olson 1996; Hone and Watabe 2010; Hone and Tanke 2015), which would result in shallower tooth traces. We suspect that the scores on SWAU HRS13997 may be a combination of *Tyrannosaurus* premaxillary teeth and lateral teeth dragging along the surface to strip flesh off of the bone, given the varying depths and orientations of scores on the bone.

There are several other examples in the fossil record of tyrannosaurid tooth traces on tyrannosaurid bones. Jacobsen (1998) noted tyrannosaurid tooth traces on tyrannosaurid bones from the Dinosaur Park Formation, which he attributed to feeding. Tyrannosaurid face-biting due to intraspecific aggression has been suggested in the literature as a cause for tyrannosaurid skulls possessing tyrannosaurid tooth traces (Tanke and Currie 1998; Peterson et al. 2009). Peterson et al. (2009) used the Extant Phylogenetic Bracket—a technique usually reserved for inferring the morphology of soft tissues in fossil organisms (Witmer 1995)—to infer such behaviors could have occurred in tyrannosaurids, since intraspecific face biting can be found in the only two extant archosaur groups: crocodilians (Peterson et al. 2009) and birds (Blanco et al. 1997). Face-biting behavior in tyrannosaurs was also suggested to explain a tyrannosaurid left dentary (TMP 1996.05.13) with a tyrannosaurid tooth lodged in it from the Dinosaur Park Formation; however, Bell and Currie (2010) were unable to determine whether the bite occurred pre- or postmortem, nor could they discern whether the biter was the same species as the victim. A skull and mandible from a skeletally immature specimen of the tyrannosaurine *Daspletosaurus sp*. (TMP 1994.143.0001) from the Dinosaur Park Formation of Dinosaur Provincial Park, Alberta, Canada appears to show both healed, premortem tooth traces and postmortem tooth traces on the mandible, all made by another tyrannosaurid (Hone and Tanke 2015). The authors attributed the premortem traces to intraspecific combat and the postmortem traces to scavenging. However, the authors were unable to determine if the scavenging was cannibalistic because of the presence of two tyrannosaurid species in the Dinosaur Park Formation, as in the case of TMP 1996.05.13 and the tyrannosaurid bones studied by Jacobsen (1998). According to Hone and Tanke (2015), the definite postmortem bite trace on the dentary was probably made by a tooth from the maxilla or non-anterior dentary of a tyrannosaurid because tyrannosaurid premaxillary teeth are more closely spaced.

Longrich et al. (2010) described four specimens of *Tyrannosaurus rex* (UCMP 137538, MOR 1126, MOR 920, and MOR 1602) from the Hell Creek Formation of Montana that possess tooth scores made by a large, predatory animal. Five furrows—called gouges by Longrich et al. (2010)—mark the proximal end of UCMP 137538, an isolated pedal phalanx. Another pedal phalanx, MOR 1126, this time from a partial skeleton, also possesses tooth traces in the form of furrows and scores with at least one containing denticle striae. MOR 920 is a left humerus that was found as part of an associated, skeletally mature *Tyrannosaurus rex* skeleton featuring several scores on its posterior surface. The final specimen they described (MOR 1602) was an isolated right metatarsal III missing the proximal half of its shaft. Two scores can be found on the medial surface. All of these tooth traces are attributed by the authors to feeding rather than fighting because the bites would have been difficult to inflict on a live animal, as three of the examples are from the feet. Additionally, at least one of the specimens (MOR 1126) was bitten more than once, and the score on MOR 1602 runs across the bone's articulation with metatarsal II. None of the bites showed any evidence of healing, which confirms that they must have been bitten shortly before, at, or after death. These tooth scores are smaller in width than others previously attributed to *Tyrannosaurus* (Erickson and Olson 1996), which led Longrich et al. (2010) to suggest they were made by juvenile or sub-adult *Tyrannosaurus* individuals (these authors consider *Nanotyrannus* to be a juvenile *Tyrannosaurus rex*). The authors reason that because they only studied a relatively limited sample of tooth-marked bones, cannibalism must have been common in *Tyrannosaurus*.

SWAU HRS13997 is also suggestive of cannibalism in *Tyrannosaurus rex*. That the tooth traces represent feeding rather than some other biting behavior is supported by four lines of reasoning. First, although it is possible that a *Tyrannosaurus* could bite the foot of another *Tyrannosaurus* in intraspecific combat, it seems unlikely, especially since there appear to be multiple bites in the same area. Second, these scores are perpendicular to the long axis of the bone, which would be expected for a feeding trace (Njau and Blumenschine 2006; Pobiner et al. 2007). Third, all of these marks are examples of scores, where the teeth are dragging along the surface of the bone, rather than pits or punctures. This means that the animal was scraping its jaw along the foot, not just simply biting it as might be expected in a combat scenario. Scores could also occur in a scenario where the feeder is dragging a carcass; however, these marks are shallow and lack pits or punctures, which is consistent with the defleshing of a bone during feeding. Fourth, the three scores in cluster 1 begin as separate traces, but then join together to form a single score (Fig. 4). This suggests that the animal is turning its head as it is biting, probably to scrape off some flesh from the bone. The combination of all of these factors suggests that the biter was indeed feeding on the other individual's foot.

Whether the larger *Tyrannosaurus* killed the smaller individual cannot be determined from the available evidence. However, considering that it would be difficult for a larger *Tyrannosaurus* to reach its jaws low enough to bite a smaller individual's foot while the smaller individual was still standing, then these bites were likely made after the smaller individual was already lying on the ground. Additionally, there would not have been a great deal of meat attached to the metatarsals, which suggests this may be a scavenging scenario where the larger tyrannosaurid is attempting to get even the smallest bits of meat off of an already picked-over carcass. A larger *Tyrannosaurus* feeding on a smaller individual could suggest infanticide, but there is no way to determine the relationship between the two individuals. Furthermore, given the similarity in size between SWAU HRS13997 and the metatarsal of LACM 23845, the small tyrannosaur would have probably been a subadult animal (Carr and Williamson 2004), which suggests it was likely living on its own without parental care for several years.

Because tyrannosaurids could and did eat bones (e.g., Chin et al. 1998, 2003; Varricchio 2001), it is unclear why the larger tyrannosaurid did not simply swallow the smaller individual's foot or at least this metatarsal whole. There does not appear to be any evidence of etching by digestive processes on SWAU HRS13997 as has been noticed in other bones ingested by tyrannosaurids (Varricchio 2001). For whatever reason, it appears that this *Tyrannosaurus* individual preferred to nip flesh off of the metatarsal rather than swallowing it whole.

CONCLUSIONS

The discovery of SWAU HRS13997, a fourth metatarsal from a small tyrannosaurid, in the Lance Formation of Wyoming, possessing *Tyrannosaurus* tooth scores on its surface, is best interpreted to be further evidence for cannibalistic behavior in this large theropod. Although cannibalism is a likely explanation for these tooth scores, it is also possible that a *Tyrannosaurus rex* was feeding upon an immature individual from a currently unknown different species of tyrannosaurid. Even if this bone does pertain to a separate species, this particular fossil presents us with insights into tyrannosaur feeding behavior. It appears that on this occasion, a *Tyrannosaurus* stripped flesh off of a bone rather than swallowing the bone whole, even when very little flesh was present. This find represents the first evidence for tyrannosaurids feeding on tyrannosaurids in the Lance Formation, as well as the first instance of *Knethichnus subparallelum* and *Linichnus serratus* on a tyrannosaurid bone. It is possible that further excavations at the location of discovery of SWAU HRS13997 may uncover more material from this small scavenged tyrannosaurid.

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SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: http://www.sepm.org/pages.aspx?pageid=332.

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