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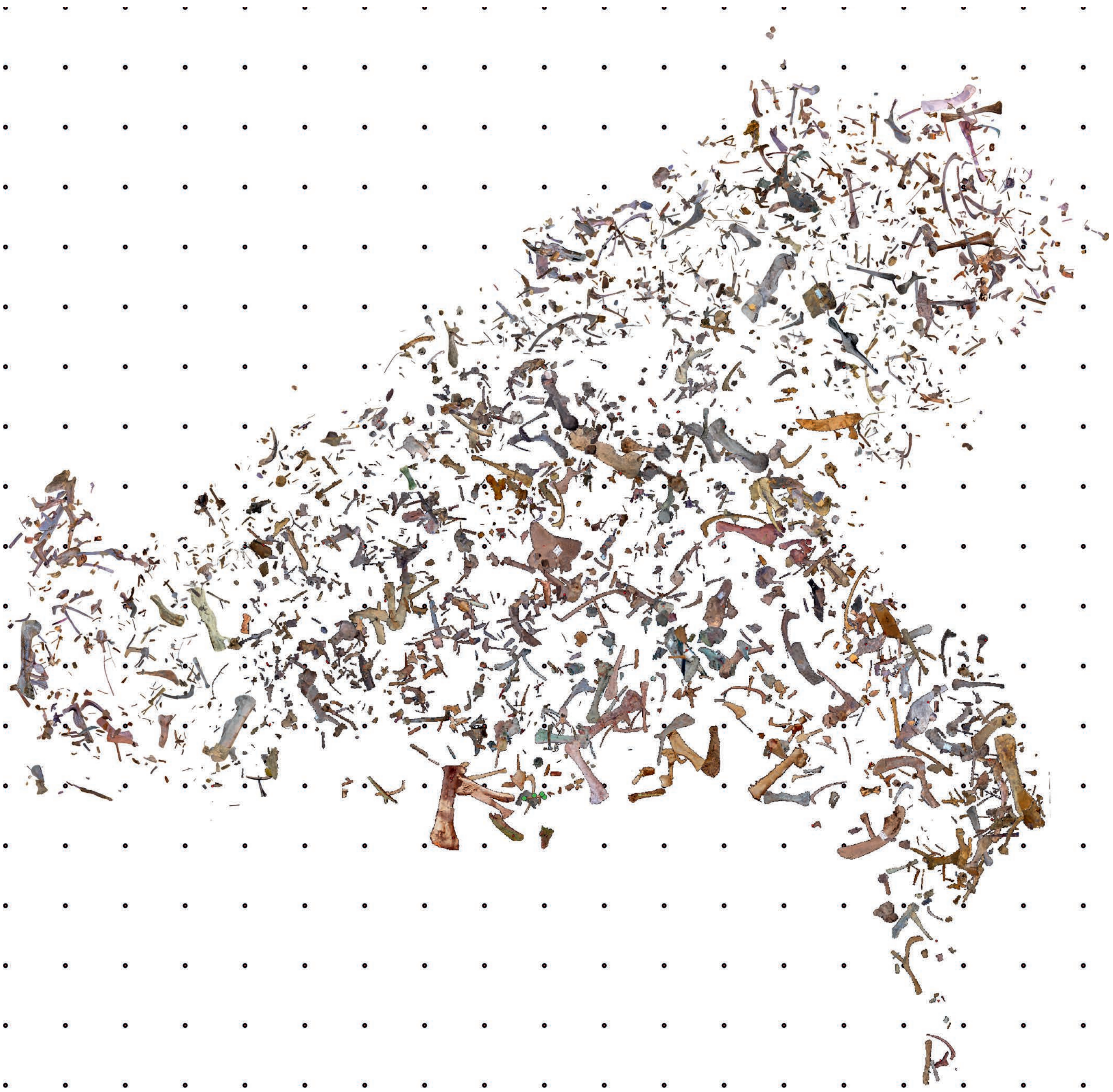

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SKELETAL TRAUMA WITH IMPLICATIONS FOR INTRATAIL MOBILITY IN *EDMONTOSAURUS ANNECTENS* FROM A MONODOMINANT BONEBED, LANCE FORMATION (MAASTRICHTIAN), WYOMING USA

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ABSTRACT: **This study presents evidence of pre-mortem traumatic injury and its sequalae on multiple *Edmontosaurus annectens* skeletal elements recovered from a largely monodominant Cretaceous (Maastrichtian) bonebed. The sample consists of 3013 specimens excavated and prepared from two quarries, of which 96 elements manifest one or more macroscopic bone abnormalities and 55 specimens display pathology attributable to physical trauma. Evidence of traumatic pathology is strongly associated ($P < .05$) with body region, occurring disproportionately in the caudal vertebrae. Pre-mortem fractures with subsequent bone remodeling and hypertrophic ossification of caudal neural spines are present principally in the middle and mid-distal regions of the tail, while fractures of the vertebral centra are present primarily in the distal tail region. Other skeletal regions, such as chevrons, phalanges of the manus and ribs display unambiguous evidence of healed trauma, but with less frequency than the tail. These findings, in combination with current understanding of hadrosaurian tail biomechanics, indicate that intervertebral flexibility within the middle and mid-distal region of the tail likely rendered these caudal vertebrae more susceptible to the deleterious effects of repeated mechanical stress and subsequent trauma, potentially accompanying running locomotion and other high-impact herd interactions. Healed fractures within the region are also suggestive of accumulated injuries due to a combination of tail usage in defense and possibly accidental bumping/trampling associated with gregarious behavior.**

INTRODUCTION

Bone pathology has long been consulted to provide evidence of life history in fossil organisms. Since Moodie (1918) provided the first extensive report of fossils and diseases of dinosaurs (also including fossils of other animals), many researchers have developed functional inferences of widely varying comprehensiveness, precision and likelihood based on dinosaurian paleopathology (Tanke 1989; Rothschild 1997; Tanke and Currie 1998; Rega and Brochu 2001; Hanna 2002; Tanke and Farke 2006; Rothschild and Tanke 2007; Farke et al. 2009; Wolf et al. 2009; Tanke and Rothschild 2010; Rega 2012; Bell and Coria 2013; Tanke and Rothschild 2014; Foth et al. 2015; Siviero et al. 2016). Challenges in the interpretation of such data are myriad and include small samples with stochastically varying temporal and spatial distribution, isolated skeletal elements and the diagnostic variation of multiple observers. In the context of the following study, the quantity of elements of a single species, temporal control and diagnostic alignment have combined to provide an opportunity for a greater degree of diagnostic confidence than usual.

When dealing with fossils, pathologies are initially diagnosed by observation of osseous manifestations that vary from the normal state. Because the material available is primarily skeletal, assessment of any disease state is necessarily limited to those conditions that ultimately affect bones, which represent only a small subset of the total possible disease states affecting individuals. Abnormal bone can be manifested in many forms: absence of bone (lysis or mediated resorption), proliferation of bone, abnormal bone architecture and/or mineralization, and non-taphonomic mechanical damage, with or without healing. These conditions can be due to traumatic injury, bone and bone-adjacent tissue proliferation and neoplasms (tumors), developmental and/or genetic conditions, infections (associated with injury or not), increases or decreases in vascular supply and/or drainage and degenerative changes such as osteoarthritis and osteophyte formation to bone, articular cartilage, ligament and tendon (Resnick et al. 1995). Determining the etiology or, more specifically, probable cause for observed pathology is important because it sheds light into our understanding on the animals' biology, morbidity, living conditions, and predisposition to diseases.

Studies of isolated specimens are most frequent in the paleopathological literature but tell only that an event or disease occurred at least once in the past (Hanna 2002; Dumbravă et al. 2016; McLain et al. 2018). Aggregation of these single studies can begin to produce behavioral data (Carpenter 1998; Tanke and Currie 1998), but those data are limited by inter-observer variation and issues of contemporaneity and environmental locational differences. Studies of complete specimens can provide more sophisticated life history while controlling for these factors. For example, Hanna (2002) reports a nearly complete *Allosaurus* specimen, where traumatic injury occurs in multiple skeletal elements suggesting separate events, indicating a lifetime of traumatic injury. Rega et al. (2010) described patterns in three *Chasmosaurus* specimens of bone injury and degeneration involving metacarpal I and phalangeal elements. These injuries were consistent with a semi-sprawled posture of the forelimbs, which contributes to the long-standing debate on ceratopsian forelimb posture during locomotion. Farke et al. (2009) studied multiple individuals from different locations and time periods to identify signs of agonistic combat utilizing horns in *Triceratops* from analysis of facial lesions.

Because of their relative ease of diagnosis, traumatic pre-mortem bone modifications associated with bone remodeling have the potential to be good indicators for interspecific and intraspecific animal behavior, especially where contemporaneous large samples allow the frequency of specific bone abnormalities in a taxon to be ascertained. Bell and Coria (2013), in their paleopathological survey of the theropod *Mapusaurus,* observed a low overall frequency of bone pathology within the bonebed, with only five bones out of 176 exhibiting abnormalities. However, when lesions were found, they were consistently similar in form and traumatic in origin. Thus, they concluded that *Mapusaurus* was highly active, often with aggressive behavior (Bell and Coria 2013). Tanke and Rothschild (2010), in a study of a large ceratopsid bonebed and isolated specimens, suggested a relationship between some pathologies and behavior. The healing fractures from injuries in the middle to posterior dorsal ribs suggested intraspecific behavior that could have occurred in acts of nonfatal side-butting (Tanke and Rothschild 2010).

Extensive availability of hadrosaurian specimens in North America enables the study and reporting of different cases of pathologies associated with these animals. Observed pathological bone abnormalities primarily from isolated specimens in hadrosaurs include: hypertrophic neural spines, pseudarthrosis (unhealed fractures), osteophytes, healed fractures, osteochondrosis, and diffuse idiopathic skeletal hyperostosis of vertebrae (Rothschild 1997; Rothschild and Tanke 2007; Rega 2012; Tanke and Rothschild 2014). The most frequent pathology noted in hadrosaurs is pre-and perimortem fractures and hypertrophic ossification of neural spines in caudal vertebrae (Rega 2012; Tanke and Rothschild 2014), which suggests as causal factors hadrosaurian behavior and biomechanics associated with the tail.

Different interpretations of the sources of tail injury depend on the location and context of trauma. Some speculative interpretations of the preponderance of tail injuries include: attempted predation trauma associated with tail (Carpenter 1998; De Palma et al. 2013), proximal caudal vertebrae injury due to trauma during mating (Rothschild and Tanke 1992), trauma due to sudden turn or swing of its tail in herds, defense from predators and crushed caudal centra suggesting trampling by nearby animals (Tanke and Rothschild 2014). Although some of these might be plausible explanations, the scientific community has dismissed others (Tanke and Rothschild 2014).

In the northwestern United States and southwestern Canada, two species of hadrosaurs are recognized. *Edmontosaurus regalis* appears to be limited to the upper Campanian and lower Maastrichtian deposits (Campione and Evans 2011; Xing et al. 2017). *Edmontosaurus annectens* specimens are found in the upper Maastrichtian of the Hell Creek Formation (Ullman et al. 2017) and also appear to be representative of the upper Maastrichtian deposits (Paul 2016) in the Lance, Laramie, Scholard and Frenchman Formations.

In this study, we examined the contents of *Edmontosaurus annectens* monodominant bonebed within the Cretaceous (upper Maastrichtian) Lance Formation, northeastern Wyoming which presents an ideal opportunity for the study of pathological incidence in a single population and species. The bone surfaces of the majority of elements are generally well-preserved and lack evidence of significant surface and edge abrasions due to transport. Elements are mostly disarticulated and scattered, with occasional association of elements. Small elements (e.g., phalanges, caudal vertebrae) are often preserved intact. While occasional larger elements (e.g., limb bones) are mostly complete, most are fractured post-mortem at typical break locations. Giving the homogeneity of the specimen condition, lack of indicators of abrasion or extensive exposure on the cortical surfaces, it appears that the bonebed was deposited in a single event. Further taphonomic analysis is forthcoming (K. Snyder personal communication 2017).

The minimum number of individuals (MNI) in this study is 28 (based on left surangulars excavated from 1997–2017), with primarily adults but some older juveniles represented. Younger juveniles are most certainly underrepresented in the bonebed, as only two specimens can be attributed to this category (< 0.1 % from total bones observed in this study). Despite this observation, a purely attritional origin, resulting from culling of elderly, diseased and vulnerable individuals, seems less likely given the physical environment, where the bonebed geology indicates a subaqueous debris flow (K. Snyder personal communication 2017). The age distribution of the specimens increases the chances that this sample represents at least a partial "snapshot" of the portion of the population from which it is derived. Due to mass differences, younger juveniles are frequently missing from bonebed environments, as flow dynamics affects very small individuals differently than larger ones (Voorhies 1969; Aslan and Behrensmeyer 1996). In addition, lower bone mineralization of juvenile can contribute to their lack of preservation. Although the bonebed likely represents a "snapshot" of older juvenile and adult pathology, the disease experience of young juveniles simply cannot be addressed with this sample.

In this study, abnormal bone manifestations suggestive of pathology were assessed on multiple elements. Traumatic osseous pathology is the most straightforward to diagnose in fossil samples. Hypertrophic ossification of neural spines and fractures exhibiting healing are among some of the bone lesions observed in the specimens, and they indeed comprise the majority of cases observed suggestive of stress and/or trauma. Pre-mortem bone modification due to traumatic injury directly associates modification with probable cause. Other bone modifications such as tooth traces, osteochondrosis and osteoarthritis are also found, but these are discussed elsewhere (Siviero et al. 2016) and will be the subject of forthcoming analyses from this locality.

The purpose of this study is to (1) report and describe *E. annectens* bones with pre-and perimortem trauma, and (2) to evaluate whether pre-mortem bone modifications indicative of trauma and/or stress are associated with specific body regions of *E. annectens*. To maximize diagnostic accuracy, we focused only on bones that manifest evidence of bone remodeling associated with traumatic injury, thus excluding instances of potential peri-mortem injury. We tested three hypotheses: that trauma and/or stress-related injuries occurred most frequently (1) in the vertebrae relative to other body regions; (2) in the caudal vertebrae relative to other vertebrae; and (3) in the middle to mid-distal region of the caudal vertebrae. Understanding the frequency of pre-mortem bone modifications indicative of trauma, especially when localized, contributes to a more nuanced understanding of hadrosaur behavior and tail function.

METHODS

Edmontosaurus annectens specimens from a monodominant bonebed collection excavated at the Hanson Ranch property in Roxson, northeastern Wyoming, between 1997–2017 were examined. Bones were prepared, accessioned and permanently stored at the SWAU paleontological museum. The first author evaluated all bones from the two largest quarries (Fig. 1), mostly North and South quarries (MNI = 18, left surangular), which correspond to the same bonebed. Individual bones were assigned to nine categories for analysis: (1) skull and jaw (surangular, splenial, angular, jugal, maxillary, quadratojugal, quadrate, lachrymal, nasal, squamosal, postorbital, frontal, braincase, hyoid, ectopterygoid, and premaxillary); (2) shoulder/pectoral girdle (scapula, coracoid and sternal); (3) pelvis (ilium, pubis and ischium); (4) ribs (cervical and dorsal); (5) chevron; (6) sacrum; (7) forelimb (humerus, radius, ulna and manus, including carpal, metacarpals, and phalanges); (8) hind limb (femur, tibia, fibula and pes, including calcaneus, astragalus, metatarsals, and phalanges); and (9) vertebrae (cervical, dorsal, and caudal). To determine differences between vertebrae types and distinctions along regions (from proximal to distal) of

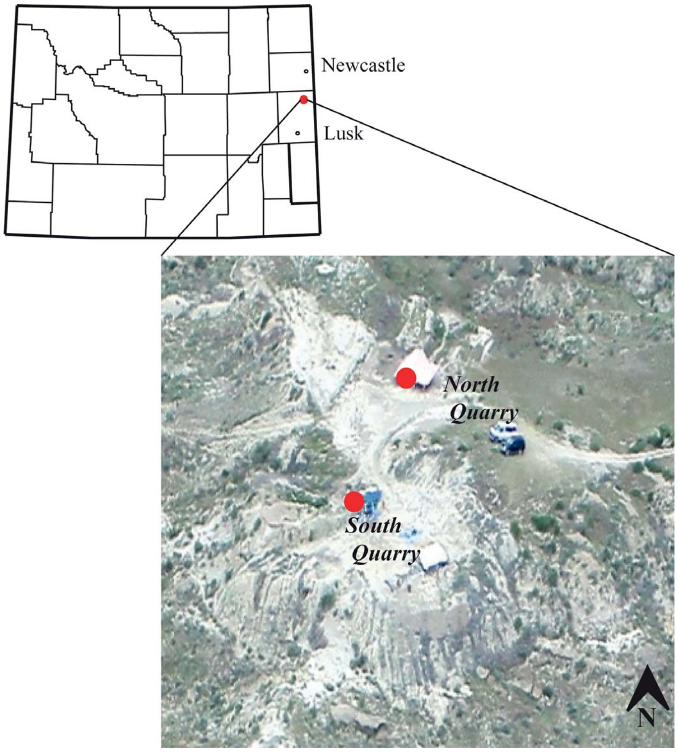

FIG. 1.—Map of the bonebed location and quarries (North and South) analyzed in this study.

dorsal and caudal vertebrae column, vertebral region was assessed according to previous descriptions by Campione (2014).

Based on macroscopic examination of bone texture and structure, the first and second authors identified specimens with bone modifications deviating from normal conditions and suggestive of pathologies. Although we identified pathologies resulting from trauma, infection, developmental defects and idiopathic causes, we consider here only those specimens manifesting evidence of pre-mortem mechanical trauma with associated bone reaction.

We photographed specimens with a Canon EOS D30 camera on a Beseler CS-21 copy stand with external lighting for better image contrast. We obtained computed tomography images at the Radiology Department at LLMC to assess (1) bone reactivity associated with trauma; and (2) deeper bone perforations associated with trauma.

For statistical analysis, we classified each bone according to evidence of pre-mortem trauma or no trauma. We conducted three two-way Pearson chi-square tests: (1) presence of trauma among the nine bone categories; (2) presence of trauma among the three vertebra types (cervical, dorsal, and caudal); and (3) presence of trauma among the five caudal vertebrae regions (proximal, proximal-middle, middle, middle-distal, and distal vertebrae; Fig. 2). For the first and third analyses, more than 20% of the cells had expected frequencies < 5, which violated an assumption of chi-square tests; however, we reported results anyway because collapsing categories to meet the assumption (to six bone categories and three caudal vertebrae categories) gave essentially identical results. We computed effect sizes as Cramer's V, with small, medium, and large effects loosely corresponding to ~ 0.1, ~ 0.3, and ≥ 0.5, respectively (Cohen 1988). Following Nakagawa (2004), we chose not to adjust alpha for multiple tests because doing so overemphasizes the importance of null hypothesis testing when effect size is more meaningful, and unacceptably increases the probability of making type II errors (i.e., the hyper-Red Queen phenomenon: the more research one does, the lower the probability that a significant result will be found; Moran 2003). We analyzed our data using SPSS 23.0 for Windows (Statistical Package for the Social Sciences, Inc., Chicago, Illinois, USA), with alpha set at 0.05.

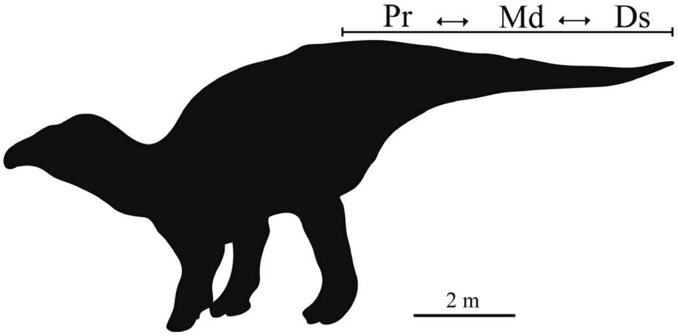

FIG. 2.—Lateral view of tail regions of *Edmontosaurus annectens* outline illustration.

INSTITUTIONAL ABBREVIATIONS

HRS, Hanson Research Station, Roxson, WY; LLMC, Loma Linda Medical Center, Loma Linda, CA; SWAU, Southwestern Adventist University, Keene, Texas

RESULTS

Out of a total of 3013 bones visually examined by first author (North and South quarries, Table 1), 55 specimens exhibited bone lesions indicative of pre-mortem trauma and/or reactive bone response. Provisional diagnosis was determined by first author and refined in collaboration with the second author on the actual specimens: two ribs, four chevrons, two phalanges of the manus, three dorsal vertebrae, and 44 caudal vertebrae (Table 1). Evidence of trauma in bones included: (1) fracture with bone remodeling; (2) fusion of associated bones; (3) hypertrophic ossification; (4) tooth traces (with associated bone remodeling); and (5) undetermined trauma associated with bone remodeling. A few specimens with trauma manifest angulation/non-alignment of bone parts in the process of healing and/or infection. Pre-mortem trauma in the sample, appeared to be at different stages of healing, from early to advanced osseous healing. Pre-mortem trauma was more obvious or dramatic when in association with early bone remodeling than when healing was completed or advanced. If no healing was present, any observed trauma was designated perimortem and not included in the analysis, as immediate post-mortem damage cannot be ruled out absent healing.

Description of Representative Bones Bearing Pre-Mortem Trauma

Table 2 provides a complete list of all specimens examined manifesting bone trauma and/or modification reported in this study. For images of each specimen, see the online SWAU fossil catalog available at https://fossil.swau.edu. To document the range and types of trauma, several specimens are further documented below. Reactive bone lesions secondary to potential bite injury (HRS09477, HRS01295; Table 2) have been included in this analysis for completeness; however, diagnosis of tooth traces is not the primary object of this study. A forthcoming analysis will be dedicated to tooth trace evidence from this locality.

Vertebrae.—Specimen HRS07948: neural spine from a middle-distal caudal vertebra (Fig. 3) with bone remodeling (callus) on the distal neural spine showing macroscopically visible fracture plane. In the remodeling region, two large perforations of the cortical bone covering are readily

TABLE 1.—*Bones examined per body region for pre-mortem trauma and mechanical stress. Abbreviations: CATG = bone category; SCATG = bone subcategories; TC = total count; TrC = trauma count; prox-mid = proximal-middle region; mid-dist = middle-distal region. Trauma count only includes pre-mortem trauma.*

CATG	SCATG	TC	TrC	CATG	SCATG	TC	TrC
Head		256	0	Forelimb		192	2
	Premaxillary	10	0		Humerus	11	0
	Ectopterygoid	13	0		Radius	12	0
	Hyoid	12	0		Ulna	13	0
	Braincase	5	0		Metacarpal	50	0
	Frontal	15	0		Carpal	3	0
	Post-orbital	18	0		Phalanx manus	103	2
	Squamosal	14	0	Hindlimb		177	0
	Nasal	19	0		Femur	20	0
	Lachrymal	14	0		Tibia	12	0
	Quadrate	25	0		Fibula	26	0
	Quadratejugal	20	0		Calcaneous	3	0
	Maxillary	11	0		Astragalus	12	0
	Jugal	19	0		Metatarsal	26	0
	Angular	18	0		Phalanx pes	78	0
	Splenial	18	0	Vertebrae		1312	47
	Surangular	25	0		Cervical total	43	0
Shoulder		52	0		Dorsal total	93	3
	Scapula	31	0		a) dorsal (proximal)	7	1
	Coracoid	8	0		b) dorsal (prox-mid)	36	1
	Clavicle	13	0		c) dorsal (middle)	35	1
Pelvis		81	0		d) dorsal (mid-dist)	3	0
	Ischium	31	0		e) dorsal (distal)	12	0
	Pubis	45	0		Caudal total	588	44
	Ilium	5	0		a) caudal (proximal)	9	0
Rib		546	2		b) caudal (prox-mid)	22	1
Chevron		394	4		c) caudal (middle)	53	15
Sacrum		3	0		d) caudal (mid-dist)	107	21
					e) caudal (distal)	397	7

TABLE 2.—*Individual bones exhibiting modifications suggestive of pre-mortem trauma and mechanical stress. Abbreviations: AG = angulation (non-alignment); BR = bone remodeling (general); FR = fracture, FU = fusion; HPO = hypertrophic ossification; INF = infection; TT = tooth trace; UT = undetermined trauma.*

Bone type	Modification	Bone type	Modification
Manual Phalanx		Vertebra	
HRS07257	BR, UT	Caudal (cont.)	
HRS02079	BR, UT, INF	○ middle	
Chevron		HRS06606	BR, HPO
HRS00853	BR, FR	HRS02082	BR, FR, HPO
HRS17086	BR, FR	○ middle-distal	
HRS07815	BR, FR	HRS07245	BR, FR
HRS05154	BR, IT	HRS05551	HPO
Rib		HRS00428	BR, FR
HRS17249	BR, FR	HRS10014	BR, UT
HRS09477	BR, TT	HRS03360	BR, UT
Vertebra		HRS14325	HPO
Dorsal		HRS27044	HPO
○ proximal		HRS01106	BR, FR
HRS00727	HPO	HRS00081	BR
○ proximal-middle		HRS01248	BR, FR
HRS05892	BR, UT	HRS05579	AG, BR
○ middle		HRS00881	HPO
HRS08259	AG, BR	HRS09546	AG, BR
*HRS01295	BR, FR, TT	HRS05807	AG, BR, FR
Caudal		HRS02506	BR
○ proximal-middle		HRS09631	BR, FR
HRS00481	HPO	HRS03956	AG, BR, UT
○ middle		HRS04197	AG, BR
HRS00836	BR, FU	HRS07116	HPO
HRS12809	HPO	HRS12380	BR,UT
HRS12588	BR, FR, HPO	HRS07948	BR, INF, FR
HRS04187	AG, HPO	○ distal	
HRS07034	AG, BR	HRS07982	AG, BR, UT
HRS02738	AG, BR	HRS12758	BR, FR
HRS01427	BR	HRS05801	HPO
HRS15136	AG, BR, FR	HRS00404	BR, FR
HRS10288	AG, BR	HRS00444	BR, FR
HRS14435	AG, BR, FR	HRS00323	BR, FR
HRS05136	BR	HRS05386	BR, FU
HRS01090	AG, BR, FR, HPO		
HRS14073	BR, FR		

* Described for trauma but not used in statistical analysis due to uncertain vertebrae location (either dorsal or proximal caudal).

observed macroscopically. CT imaging shows the perforations to be deep and interconnected, forming channels through the underlying cancellous bone suggestive of cloacae (Fig. 3D–3I). Cloacae in bones are defined as drainage channels formed during the healing process from infections and are often associated with pus formation subsequent to trauma (Aghababian and Conte 1980; de Souza Barbosa et al. 2013).

Specimen HRS02082: neural spine from a middle caudal vertebra (Fig. 4). Bone remodeling on the distal neural spine is identified as hypertrophic ossification, with no macroscopically evident associated fracture evident. However, on the proximal end of the same neural spine, bone remodeling takes the form of a callus associated with a fracture plane. An approximately 20-degree angulation from the sagittal plate is also apparent at the fracture site (Fig. 4C, 4E). Associated with the callused region, a distinct bone depression suggests vascularization at the injury site associated with the healing process. CT scan images confirm fracture plane on proximal end of neural spine (Fig. 4B, 4E). Images also indicate that the depression associated with callus penetrates deep into the bone (Fig. 4D, 4E) thus, confirming external depression to be of vascular nature associated with bone healing (Fig. 4E). Bone reactivity (remodeling) in the CT scan images is indicated by the relatively denser radio-opaque regions within the traumatic sites on both ends of the neural spine (Fig. 4D, 4E).

Specimen HRS00428: middle-distal caudal vertebra (Fig. 5A) with apparent bone remodeling on the distal end of the neural spine suggesting that the terminal tip of the spine is entirely absent.

Specimen HRS01106: neural spine from a middle-distal caudal vertebra (Fig. 5B). Bone remodeling is apparent on the distal end of the spine, and the most distal portion appears to be absent, similar to specimen HRS00428 (Fig. 5A). The etiology of the missing distal portion of the spine could be attributed to pseudarthrosis, fracture at the soft callus stage, or traumatic excision of the distal spine.

Specimen HRS05801: distal caudal vertebra (Fig. 6A) with a fracture caught in the process of healing observed on the distal surface of the centrum. The reactive bone indicative of remodeling is subtle but clearly and associated with the fracture. CT scan imaging confirms the fracture plane with associated bone reaction/remodeling (denser bone) indicated by brighter regions (Fig. 6B–6D).

Specimen HRS00323: distal caudal vertebra (Fig. 6E, 6F) with a fracture of the centrum. The fracture is located on the distal surface of the centrum with associated bone remodeling on the inferior surface of the centrum (Fig. 6F). This specimen is very similar to HRS05801. Other specimens with centrum fractures include HRS12758 (distal caudal vertebra), HRS00444 (distal caudal vertebra), and HRS07245 (middle-distal caudal vertebra).

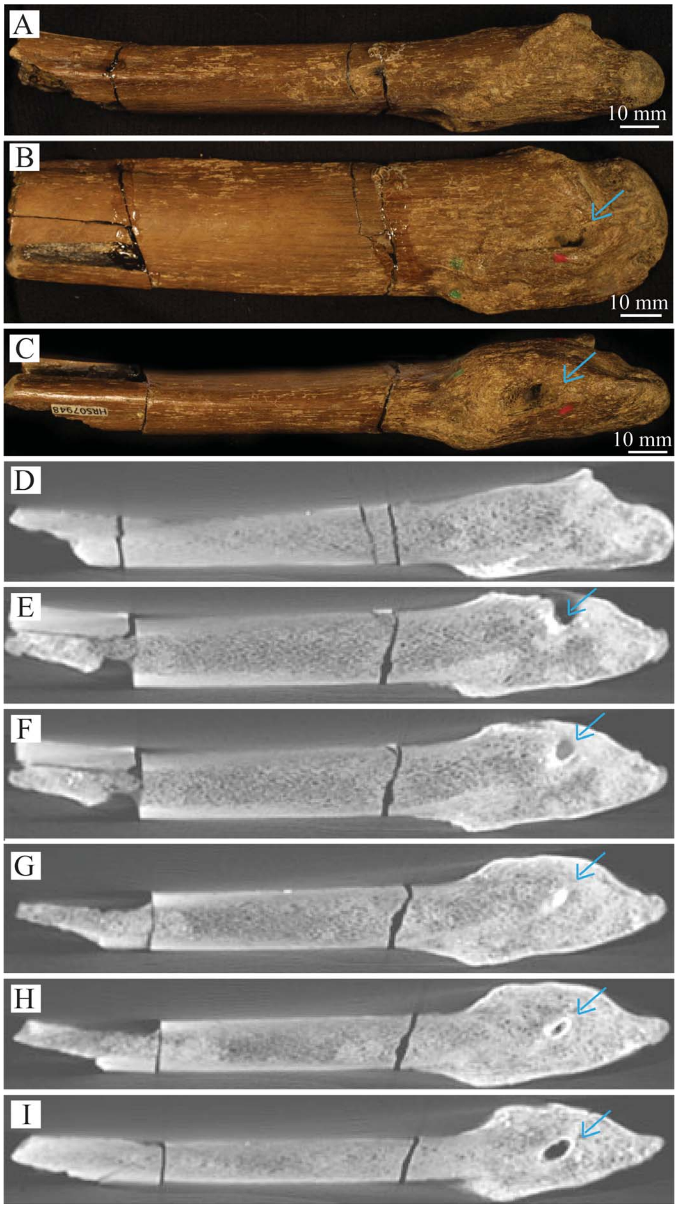

FIG. 3.—Neural spine HRS07948 manifesting lesions indicative of drainage (from a caudal vertebra within the mid-distal tail). **A–C**) Photographs of affected bone surfaces. **A**) Cranial view. **B**) Lateral view. **C**) Caudal view. Arrows indicate lesions. **D–I)** Sequence of CT scan images in serial coronal section from cranial (D) to caudal (I). Arrows indicate lacunae of continuous passage between serial sections.

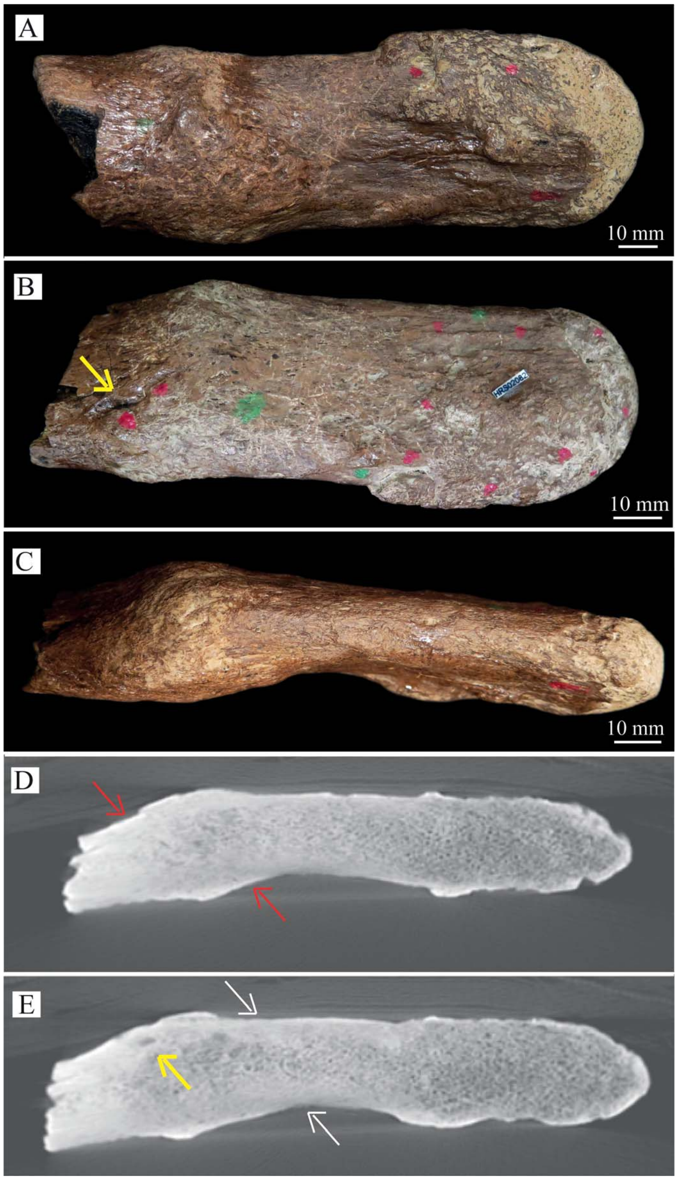

FIG. 4.—Neural spine HRS02082 from a caudal vertebra within the middle tail region. **A**) Lateral oblique view. **B**) Lateral view. **C**) Cranio-caudal view. **A–C**) Shows hypertrophic ossification on the distal end of the neural spine and bone remodeling (callus) associated with fracture on its proximal end. Yellow arrow indicates bone perforation/channeling associated with callused region. **D**, **E)** Sequence of CT scan images in serial coronal section from cranial (D) to caudal (E). Red arrows indicate fracture plane with bone remodeling association. White arrows indicate bone remodeling associated with angulation from healing fracture and possibly with hypertrophic ossification. Yellow arrow points to the same perforation from 4B suggesting continuity with surface. See text for further explanation.

Specimen HRS01295: distal fragment of neural spinal (7A). From the shape and width of the spinal fragment, we can identify the fragment to either dorsal or proximal region. We excluded this specimen from statistical analysis due the inability to specify the region more precisely. On the fracture plane/ surface of the neural spine, bone remodeling with proliferation is apparent and indicative of trauma, possibly of pseudoarthrosis or “false joint” (7A). This manifestation suggests failed fracture repair caused by movement and breakage of the soft callus investing the healing fracture prior to its mineralization.

Specimen HRS00404: neural spine from a distal caudal vertebra (Fig. 7B, 7C). On the distal neural spine, the fracture site is characterized by the non-alignment of fragments and is associated with macroscopically visible bone texture indicating bone remodeling (callus). Hypertrophic ossification is also indicated by the rugose texture (Fig. 7B, 7C) of the bone in the same region of the fracture and callus.

Specimen HRS01248: neural spine fragment from a middle-distal caudal neural spine with a large callus on its proximal end (Fig. 7D). Callus orientation indicates that it was most likely formed as a result of a fracture. Bone is well aligned at the trauma site.

FIG. 5.—Caudal neural spines with bone remodeling on distal end from mid-distal tail region. **A**) Caudal view of HRS00428. **B**) Lateral view of HRS01106. Red arrows point to area of bone remodeling.

Specimen HRS14435: middle caudal vertebra with a neural spine fracture and associated callus (with sharp fracture plane in the process of healing at time of death) on the middle region of the spine (Fig. 8A, 8B). The non-alignment of fractured bone during healing is indicated by the observed neural spine angulation.

Specimen HRS00836: middle caudal vertebra with missing neural spine and fusion of the right head of associated fractured chevron on the posterior vertebral facet (Fig. 8C, 8D). Bone remodeling from the fusion of the vertebra and the chevron is observed on its lateral surface.

Other Bone Types.—Specimen HRS00853: chevron fragment (Fig. 9A) with an obvious non-aligned fracture plane with associated callus on the distal end of the chevron. Associated with the callused region, a bone perforation is apparent possibly indicating channel for pus drainage or caseating granuloma (when infected). It also possibly indicates evidence for vascularization associated with lesion site when it was healing.

Specimen HRS17086: chevron fragment with the bifurcated end mostly complete (Fig. 9B). Fracture with associated callus is unilateral (after bifurcation) and proximal to bifurcation. CT scan images confirm fracture plane associated with callus (Fig. 9C).

Specimen HRS07257: phalanx of the manus with apparent bone remodeling on its superior and inferior cortical surfaces (Fig. 10A). CT scan imaging also indicated cortical bone remodeling noted by the apparent original bone surface plane with the new bone deposition/reaction (Fig. 10B, 10C). The newer bone has different structural alignment than the original bone. No fracture plane is observed in association with bone remodeling. However, due to bone type and location of remodeling, bone reaction resulted from most likely trauma/stress of the manus, possibly related to puncture.

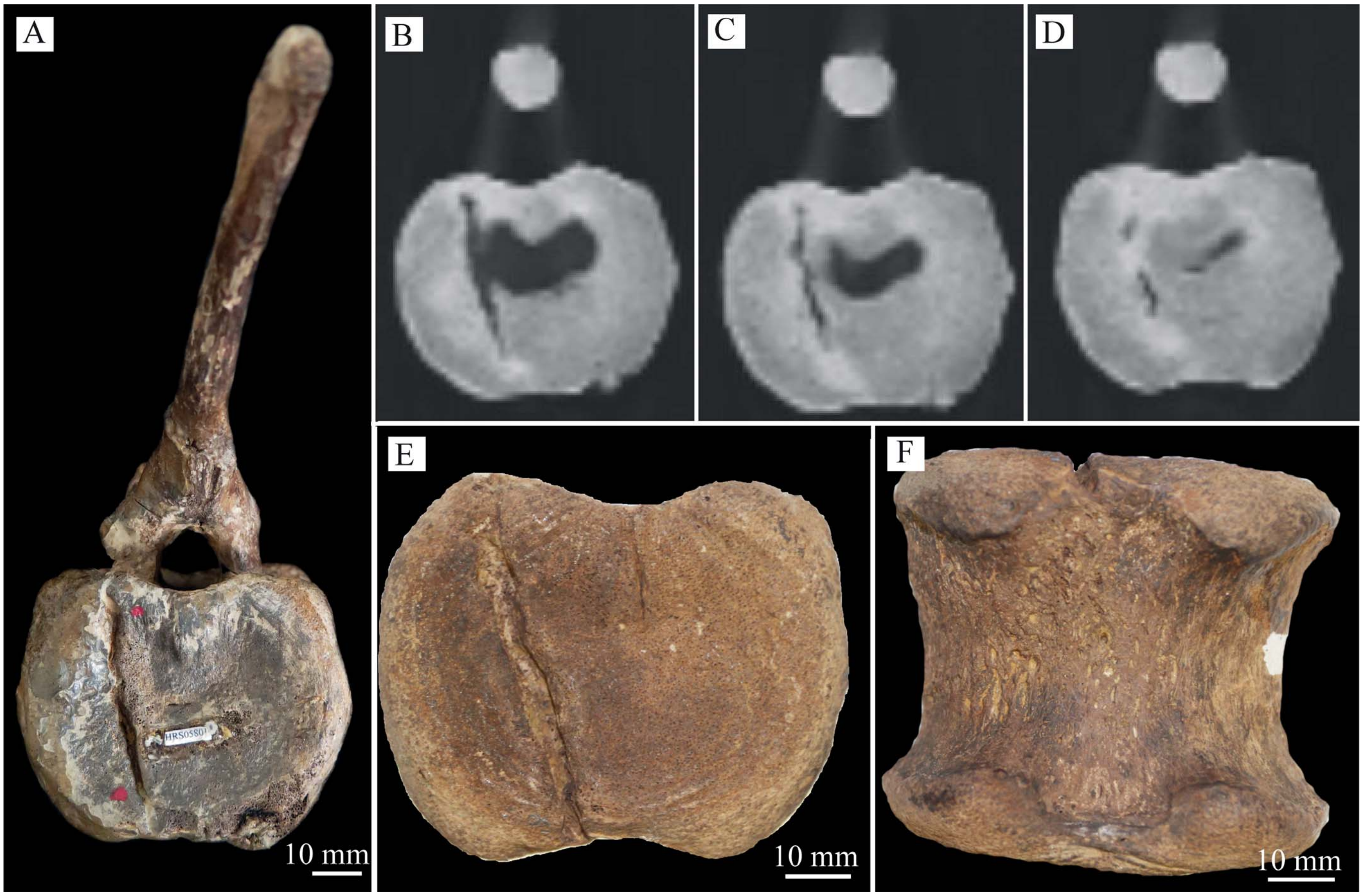

FIG. 6.—Caudal vertebrae within the distal region of the tail with pre-mortem centrum fracture. **A**) Caudal view of specimen HRS05801. **B**–**D**) Serial CT scan imaging of centrum from caudal (B) to cranial (D). **E**) Caudal and **F**) ventral views of specimen HRS00323 with centrum fracture and associated bone remodeling on ventral surface as observed on 6F.

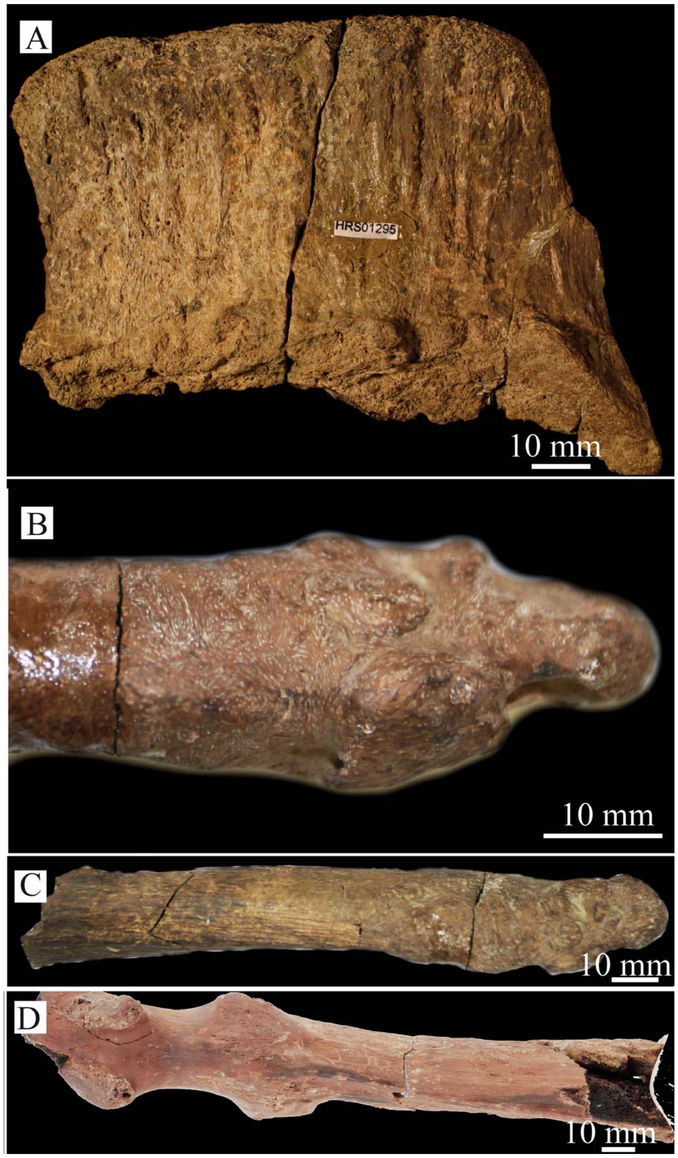

FIG. 7.— Different vertebrae with bone modifications indicative of pre-mortem trauma **A**) Lateral view of neural spine fragment HRS01295. Bone remodeling on fractured surface. **B**, **C**) HRS00404 mid-distal neural spine with mild hypertrophic ossification, and fracture with bone remodeling observed on the distal end of the spine. **B**) Magnified view (7C) of distal end of the neural spine. **C**) Lateral oblique view of HRS00404. **D**) Cranial view specimen HRS01248 caudal vertebra within the middle-distal region of the tail. Specimen has fracture with large associated callus.

Statistical Analysis of Bones with Trauma

Chi-square results indicated a weak but significant association between presence of trauma and bone category ($X^2 = 41.77$, df = 8, $p < 0.001$, $V = 0.118$). Vertebrae exhibited the highest frequency of injury (3.6%; Fig. 11A). We detected no injuries to head, shoulder/pectoral girdle, pelvis, sacrum, and hindlimb bones. Injuries were similarly distributed among the vertebrae types, but approached significance ($X^2 = 5.57$, df = 2, $p = 0.062$, $V = 0.088$), with caudal vertebrae showing the highest frequency of injury (7.5%), followed by dorsal (3.2%) and cervical (0%; Fig 11B). Within the tail, there was a moderate-to-large association between trauma and region ($X^2 = 72.74$, df = 4, $p < 0.001$, $V = 0.359$), which can be attributed to the high percentage of trauma found in the middle (28.3%) and middle-distal (19.6%) caudal vertebrae (Fig. 11C).

DISCUSSION

When accompanied by unambiguous evidence of bone remodeling/reaction, injuries indicative of trauma and mechanical stress can be some of the most easily diagnosed in fossils and the most useful for behavioral inference. Most paleopathology studies attempt to describe and diagnose pathology based on comparison with extant animals and infer thereby accompanying pathogenesis and behavioral causation. Consistent with other studies of hadrosaurian paleopathology (Rothschild and Tanke 1992; Carpenter 1998; Rega 2012; De Palma et al. 2013; Tanke and Rothschild 2014), traumatic injuries to caudal vertebrae represent a substantial fraction of the overall pathology in this *Edmontosaurus* bonebed.

Diagnosis of Infectious Response

Several observations in this study have additional importance. First, this study contributes further evidence that in at least some instances, the osseous response to infection in *E. annectens* resembles that characteristic of mammals. Among extant animals, liquid pus formation is considered a mammalian response, with reptiles and birds mounting a response characterized by the formation of solid caseating granuloma (Montali 1988; Antinoff 1997; Tell et al. 2004). Strong arguments have been made for the use of phylogenetic bracketing in paleopathology (Foth et. al. 2015) and multiple examples of osteomyelitis in dinosaurs have been suggested to have a similar response to infection as observed in extant reptiles and birds (García et al. 2017; Xing et al. 2018). However, evidence suggests that channel formation, more typically associated with pus formation in mammals, is also present in extant birds (Tully et al. 1996), extinct reptiles (Reisz et al. 2011) and multiple dinosaurian taxa (Hanna 2002; Rega 2012; Bell and Coria 2013). Hunt et al. (2019) underscore the complexity of osteomyelitic pathogenesis and subsequent bone response among vertebrate taxa. Their study of *Tenontosaurus tilletti* found an example best characterized as Brodie's abscess resulting from hematogenous dissemination of osteomyelitis. This effect on bone is rare in the veterinarian literature, but still present in birds and may well be the cause of such lesions in non-avian dinosaurs. Moreover, whether liquid pus is truly required for osseous channels to form or whether a granuloma can create the same bone response remains unanswered.

The Tail is Most Frequently Injured

To answer questions on hadrosaur behavior associated with its tail (specifically *E. annectens*) we focused only on bones that had evidence of bone remodeling associated with trauma/stress. Bones with indications of perimortem trauma can be suggestive of cause of death, especially in the case of predation. However, perimortem bone trauma can be mistaken as early post-mortem trauma in cases of scavenging. Therefore, for the purpose of this study, we concluded that pre-mortem evidence of bone trauma (with associated bone remodeling) has the potential to be more diagnostic of trauma/stress with suggestions to tail-related animal behavior, and restricted our analysis to these cases.

Analysis of trauma/stress occurrence in *E. annectens* from our bonebed collection is compatible with other previous reports of hadrosaur paleopathology (Rothschild and Tanke 1992; Carpenter 1998; Rega 2012; De Palma et al. 2013; Tanke and Rothschild 2014) which suggest that caudal vertebrae are more frequently injured compared to other bone types. The comparisons of injury frequency do need to take into account the relative abundance of caudal vertebrae as an element to be counted. The number of caudal vertebrae in hadrosaurs varies from 50–70 depending on species (Horner et al. 2004; Tanke and Rothschild 2014).

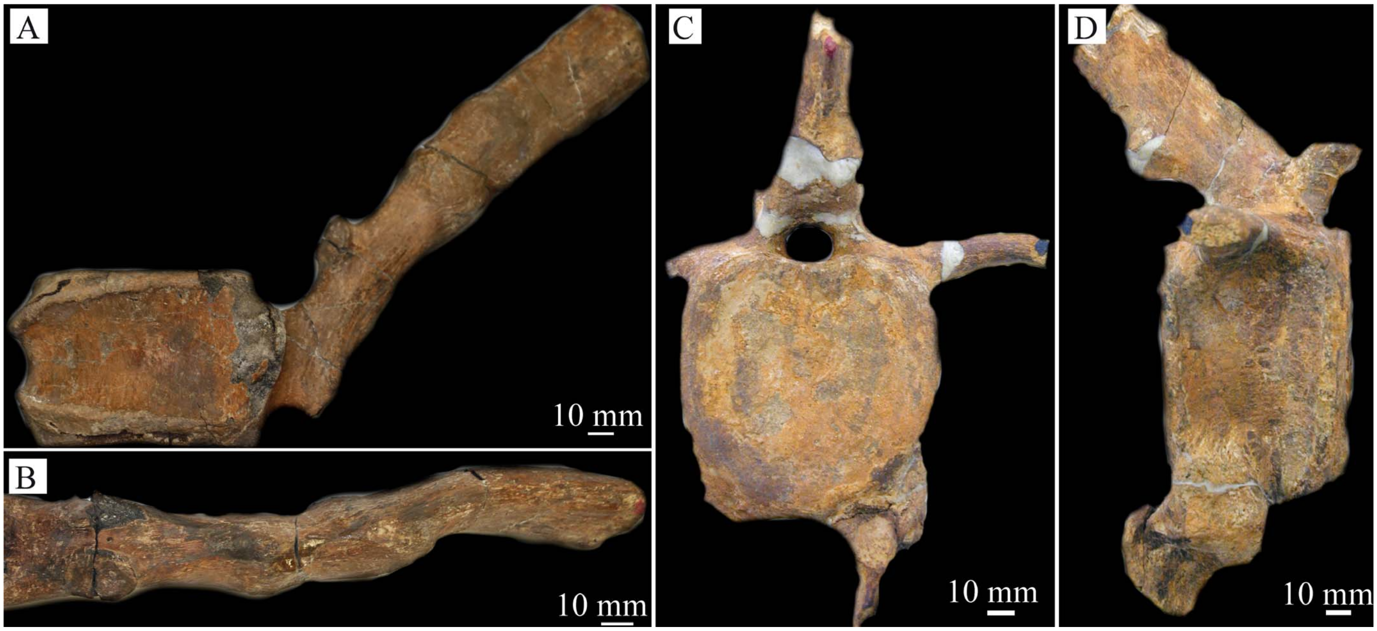

FIG. 8.—Different vertebrae with bone modifications indicative of pre-mortem trauma. **A**) Lateral view specimen of HRS14435 caudal vertebra within the middle region of the tail. Neural spine has fractures with associated calluses. **B**) Magnified caudal view of neural spine from 8A. **C**, **D**) Caudal and lateral views of caudal vertebra HRS00836 from the middle region of the tail with bone fusion of fractured associated chevron.

Elements occurring in multiples such as vertebrae are at risk of being "overcounted" in such analysis, in that there are only two femora per hadrosaur, but many more vertebrae. Therefore, for every two injured femora, there should be 50–70 injured caudal vertebrae, assuming the frequency of injury is identical. In our sample the injury counts in caudal vertebrae did also exceed this null expectation by an order of magnitude. However, we have refined this methodology by tabulating the trauma frequencies of different regions of the tail, allowing us to infer functional tail specific etiologies based on comparative regional frequency (Tables 1, 2).

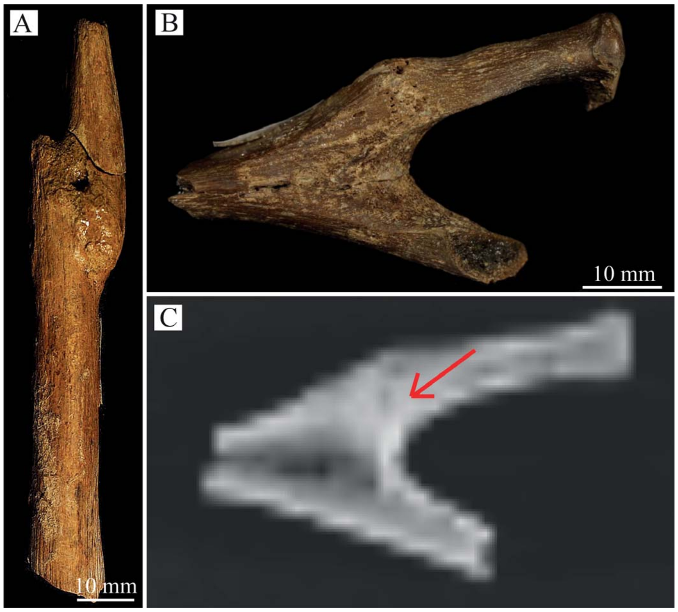

FIG. 9.—Cranio-caudal views of chevrons with healed pre-mortem fractures. **A**) Specimen HRS00853 fracture with healing (callus) and non-alignment of the distal end. Note the bone perforation associated with bone remodeling area possibly indicative of a cloaca for pus drainage or caseating granuloma inclusion. **B**) Specimen HRS17086 with post-bifurcation unilateral fracture with associated bone remodeling. **C**) CT scan imaging for specimen on Figure 9B. Red arrow points to site of healed fracture. Note fracture plane.

The low frequency of pre-mortem trauma in the majority of the skeleton, in comparison with caudal vertebrae, may be due to the relatively non-violent nature of hadrosaurian intraspecific interactions. Alternatively, this could be the product of a sampling bias in the bonebed itself, in that individuals suffering injuries to these elements did not survive an initial assault or weakened and may not have made it into the mass mortality sample represented by the bonebed. Such attritional kills may therefore be missing from the sample entirely. Such events may account in part for the paucity of bones from juveniles as well.

The low frequency of pre-mortem trauma observed in forelimbs (with single instance of affecting the phalanx of the manus) may indicate that this area is not commonly injured. The rib pre-mortem trauma is more commonly observed than forelimb. These instances could result from a fall, flank butting, or as a result of injury in an attempt to escape predation. Complicating the matter is the fact that most ribs in the sample had their distal end missing (with no evidence of bone remodeling), and with appearances of fresh bone fracture, suggestive of predation or scavenging. These missing areas may have manifested fractures which are uncounted in this analysis,

In contrast with other body regions, the spine displays the highest percentage of bone trauma and associated healing. Within the three vertebral regions, no evidence existed of pre-mortem trauma with healing among the cervical vertebrae. This may equally be the result of low actual cervical trauma or of animals subjected to cervical trauma not surviving to enter the bonebed depositional environment. Cervical trauma might be associated with a higher risk of immediate death, with no opportunity for bone remodeling to occur.

The high incidence, type of injuries, and association of trauma with caudal vertebrae is important for interpretations regarding the animal's use of its tail. Within the caudal vertebrae region, the middle to mid-distal

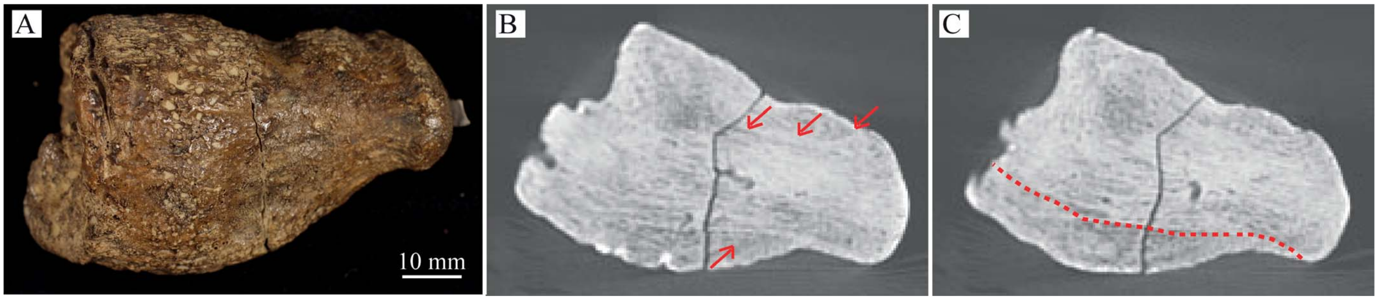

FIG. 10.—Phalanx of the manus HRS7257 with pre-mortem bone modification. **A**) Lateral view of the phalanx indicating bone remodeling on inferior and superior bone surface. **B**, **C**) Parasagittal CT scan images indicating normal bone structure with associated bone remodeling surfaces. Red arrows and traced line points to the area of transition between normal bone surface and remodeled surface. See text for further explanation.

region of the tail is especially subject to injury. Unlike injuries present in the dorsal vertebrae region, higher levels of tail pathology suggest an association with biomechanical stress. Thus, it is important to first review hadrosaurian tail structure and biomechanics.

The Role of Biomechanical Stress in Tail Injury

The study of the hadrosaurian tail musculoskeletal anatomy indicates that hadrosaurs had moderate sized epaxial muscles (spinalis and longissimus) and large hypaxial muscles (Fig. 12A, 12B) specifically the caudofemoralis (Persons and Currie 2014). Attachment of these muscles has significant biomechanical implications and is interpreted to be essential for endurance during hadrosaur locomotion (Persons and Currie 2014).

Hadrosaurian caudal epaxial muscles are attached to the caudal rib (transverse process) and corresponding caudal neural spine. The hypaxial muscles in the tail are attached to the caudal rib (transverse process) and to the corresponding chevron (on lateral surface). In hadrosaurs, hypaxial muscles in the tail are also attached to the fourth trochanter in the middle section of the femur. Caudal ribs are present only up to the middle to middle-distal region of the tail. Thus, the caudofemoralis muscle (hypaxial) tapers along the tail and is only present up to the middle region of the tail (Fig. 12A, 12B).

It has been interpreted that hypaxial muscles, especially the caudofemoralis, are necessary to keep the tail in suspension, since it is attached to the vertebra, caudal rib, chevron, and femur (fourth trochanter) (Organ 2006; Persons and Currie 2014). Because of caudofemoralis attachment to the middle section of the femur, Persons and Currie (2014) suggested that femoral retraction is slower compared to that of their predator *Tyranossaurus rex* (caudofemoralis femur attachment in *T. rex* is more proximal). Thus, in hadrosaurs, the arc of excursion of the fourth trochanter is long, and the caudofemoralis muscle is correspondingly longer and less bulky, suggesting larger excursion but less power. In the context of predator-prey interactions, hadrosaurs may have reduced stride length to preserve energy, and consequently became adapted to endurance running (Persons and Currie 2014). Thus, hadrosaurs may have had an advantage over *Tyrannosaurus,* since they could run efficiently and for a much longer period than their predator.

Anatomical factors associated with the hadrosaur tail contribute to proximal tail stability. Such factors are muscle location and attachment, bone shape and arrangement, and the presence of localized ossified tendons (Fig. 12C). Large hypaxial (caudofemoralis) and epaxial muscles within the proximal to proximal-middle region of the tail provided support and stability for the tail. Proximal tail stability is also indicated by the caudal vertebrae orientation. The caudal pre- and postzygapophyseal vertebral articulation has an inward and outward orientation respectively, thus limiting mediolateral movement (Campione 2014). In addition to the muscular and vertebral articulation, ossified tendons also contributed to the stability of the tail proximally. Among hadrosaurs, the typical lattice-work of ossified tendons extends up to the middle of the tail (Fig. 12C) and prevents dorsoventral movement of the tail, but it still allows for some mediolateral movement (Horner et al. 2004). It has also been reported that the structure and location of the ossified tendons aid in locomotion (stiffening of the tail forming a lever arm for femoral retraction), supports the large body size, and consequently reduces epaxial muscular exertion (Organ 2006). We conclude that due to the combination of these anatomical factors in the proximal-to- middle region of the hadrosaur tail, the range of motion is limited in all directions, creating greater mechanical stability.

In contrast to the proximal region of tail, the middle-to-distal region is more vulnerable to mechanical stress/trauma. The lack of the strong caudofemoralis muscle and the absence of ossified tendons in this region increase flexibility, especially for dorsoventral movement. Although pre- and postzygapophyseal orientation of articulation limits mediolateral movement within the caudal vertebrae, epaxial muscles attached to the lateral aspects of the neural spines, when retracted unilaterally, can rotate the tail toward its respective side. Thus, epaxial muscles can cause slight latero-medial movement of the tail. Epaxial muscles can also be used for stability within the middle tail region to compensate for the absence of ossified tendons. We conclude that caudal vertebrae from the middle region of the tail are more susceptible to bone remodeling due to stress/trauma, especially in cases of the hypertrophic ossification of caudal neural spines. The high frequency of bone remodeling within this region of the tail found in our study is best explained by the antagonistic forces related to vertebral angle of articulation, unilateral use of the epaxial muscles, and the lack of ossified tendons in this region.

Several occurrences of hypertrophic ossification in the distal end of the neural spines from middle and mid-distal caudal vertebrae (corresponding to this region of the tail) suggest that in this region the tail was under frequent mechanical stress. We interpret that the hypertrophic ossification of the distal end of neural caudal spines is a result of periosteal proliferation as the bone reacts to the pulling of associated epaxial muscles and interspinous ligaments. These bone reactions within this specific tail region are especially intensified during running. While running, stability within the middle region of the tail is compromised by the lack of ossified tendon and termination of the caudofemoralis muscle. Thus, for stability, epaxial muscles are intensively retracted, causing the periosteum of respective neural spines to react.

The Puzzling Lack of Chevron Injury

Fractures in the distal end of the neural spines are also more prominent and frequent within the middle to middle-distal region of the tail. Unlike hypertrophic ossification due to mechanical stress, fractures in the neural spines most likely represent trauma caused by injury/accident. Intraspecific

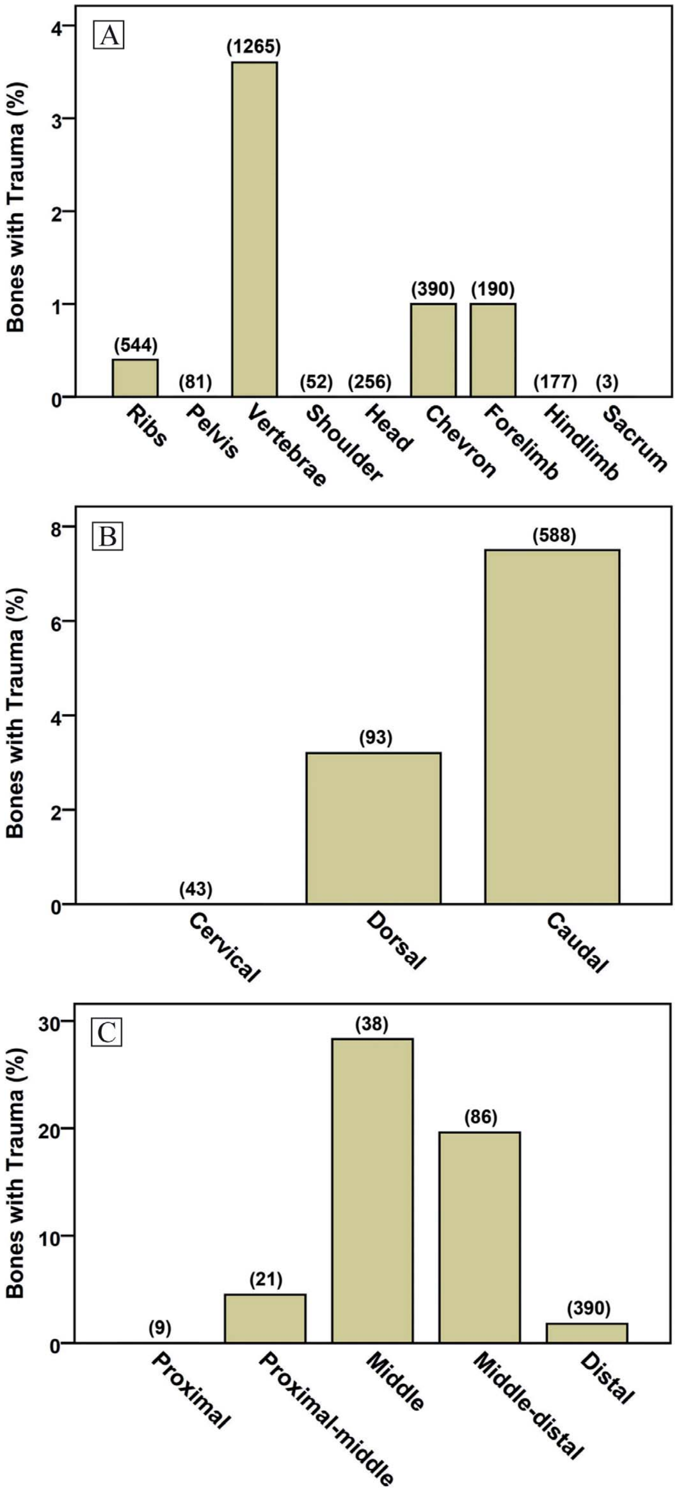

FIG. 11.—Distribution of trauma among different categories. **A**) Different bone categories. **B**) Different vertebra types. **C**) Different caudal regions. Numbers within parentheses represent total bones analyzed.

tail trampling has been previously suggested (Tanke and Rothschild 2014) as an explanation for the common tail injuries in hadrosaurs; however, one would also expect frequent fractures of associated chevrons, of which we did not find many examples. Chevrons are important bones within the tail that can suggest tail usage. Of the 394 well-preserved chevrons recovered within the bonebed, only four exhibited evidence of pre-mortem trauma. Although locating the chevron to the tail region was not possible, trauma does not seem to be present in the chevrons to the same degree as in the osseous elements dorsal to the epaxial muscles. Therefore, trampling as a reason for the high frequency of bone remodeling post-injury in caudal vertebrae seems unlikely.

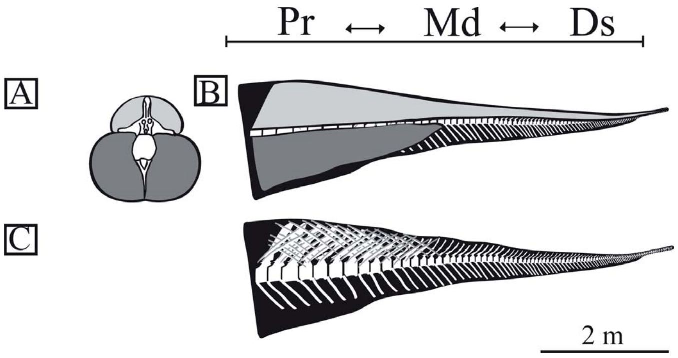

FIG. 12.—Hadrosaur tail architecture. **A**) Anterior view of the musculature arrangement from proximal tail region. **B**) Lateral view of the tail. Musculature in dark gray indicates hypaxial muscles and the light gray musculature indicates epaxial muscles. Muscle arrangement model is based on previous work by Persons and Currie (2014). **C**) Lateral view of tail skeletal arrangement with ossified tendons extending up to the middle tail. Abbreviations: Pr = proximal; Md = middle region; Ds = distal region. Arrows indicate transitional regions such as proximal-middle and middle-distal. See text for further explanation.

In further consideration of tail trampling interpretations as a cause for the frequent caudal neural spine fractures and not of associated chevrons, it is important to note the musculoskeletal structure of the tail. As previously discussed, epaxial muscles attach to the vertebral neural spines, and their mass and force exerted shaped the bones to which they were attached. Results of digital modeling of muscle attachment in the tail suggest that epaxial muscles in hadrosaurs are not particularly robust and are quite moderate in size (Persons and Currie 2014), thus making neural spines more vulnerable to fracture during trauma (Fig. 12A, 12B). However, the hypaxial muscles (caudofemoralis and ilio-ischiocaudalis) are relatively large in hadrosaurs, thus perhaps partly protecting/cushioning associated chevrons in the case of an injury. When considering the weight of the animal, even the protected chevrons would seem vulnerable to fractures during trampling. Therefore, tail trampling could have occurred, but does not fully account for the frequency and types of bone remodeling associated with the middle to middle-distal region of the *E. annectens* tail.

The Role of Interspecific Behavior in Injury

Interspecific behavior could also lead to speculative scenarios associated with the fractures. *Edmontosaururs annectens* could have injured its tail when attempting to escape from predators. In our study, we found healed tooth traces in a caudal neural spine and a rib fragment (HRS09477, HRS01295; Table 2) associated with fractures. Tooth trace injuries with evidence of bone remodeling suggest an example of escape from predation. Although such specimens are rare (bone remodeling often camouflages bite evidence), it is reasonable to conclude this scenario as one conceivable reason accounting for some of the lesions observed. A forthcoming analysis will be dedicated to tooth trace evidence from this locality.

Since *E. annectens* was apparently a gregarious animal, another credible scenario explaining frequent fractures of the caudal neural spines (especially in the middle region of tail) is trauma that some animals within the group suffered during a predator-prey chase. As groups of *E. annectens* attempted to flee from a predator attack, individuals could have suffered falls, trampling and frantic bumping into each other and into trees.

A similar scenario has been previously reported by Tanke and Rothschild (2014). Also, use of the tail as a defense mechanism when avoiding predation could explain general injury fractures, especially when considering other fractured regions along the animal's tail.

Whiplash Injuries in the Distal Tail?

In this study, centrum fracture with associated bone remodeling was mostly observed in the distal caudal vertebrae (Fig. 6). Tanke and Rothschild (2014) previously reported similar occurrences of distal caudal centrum fractures in hadrosaurs. In humans, research indicates that centrum fractures are best explained and exemplified as a result of trauma due to exaggerated movement at the articulation site, compromising the natural integrity of bone (Resnick et al. 1995). Most vertebral injuries in humans are within the thoracolumbar region due to the wide range of motion, thus resulting in frequent pure flexion, compression with flexion, and regional rotation (Pathria 1995). Instrumental to centrum fracture, and often associated with injured centrum, is intervertebral disc degeneration (Christiansen and Bouxsein 2010) or discovertebral junction trauma (Resnick et al. 1995). Such degenerations or traumas of vertebral joints may weaken the vertebral body to fracture and possibly cause a vertebral fracture cascade (Christiansen and Bouxsein 2010). Research further indicates that extensive repetitive mechanical stress within vertebrae joints may cause bone necrosis and lesions in the vertebral body in humans (Barile et al. 2007) and other animals (Revel et al. 1992).

Application of biomechanical principles and trauma causation from human studies to animal fossils greatly benefits our understanding of how the animals lived, what conditions affected their health, and how they moved and interacted with each other. In our study, distal centrum fractures were positioned in a sagittal plane with slight angulation within the vertebral anterior and middle columns. Considering the nature of the fractures, we conclude that they resulted from a combination of compression, hyperflexion, and rotation of the distal tail.

We further observed bone lesions perforating the cortical bone of several distal caudal vertebra centra (Fig. 13). These depressions had smooth edges with increased localized bone density, as indicated by brighter regions associated with depressions in the CT scan images (Fig. 13B–13D). Other examples of these are in the articulating surfaces of vertebra (restricted to lateral aspect) and occasionally also exhibited on opposing surfaces within the centrum (Fig. 13E–13G). Because of perforation morphology, location, and bone reaction associated with perforation, we interpret these types of bone perforations to be a result of regional and frequent mechanical stress that precipitated cartilaginous inclusions, and consequently localized bone sclerosis of the area within the distal region of the tail.

Although we interpret the bone depressions within the distal caudal centrum to be of traumatic nature (mechanical stress), other interpretations are also possible, such as the developmental condition osteochondrosis or even neoplasm. Previous reports of osteochondrosis in the pedal phalanx of hadrosaurs suggests potential genetic predisposition for this pathology in hadrosaurs (Rothschild and Tanke 2007). Therefore, because of other possibilities for the diagnosis of these bone lesions (traumatic vs. developmental in the case of osteochondrosis), we have not included these specimens in our statistical analysis of the distal caudal vertebrae. Regardless of whether the distal centrum bone perforations in joint surfaces resulted from frequent mechanical stress or developmental malformation, the general effect for the pathology appears to be associated with the regional (distal) centra fractures.

Because of our findings on the types of traumas within the tail of *E. annectens*, we conclude that within the distal tail region, from a combination of vertebrae joint vulnerability and frequency of distal centrum fractures, the distal tail of *E. annectens* suffered hyperflexion, compression, and fracture injuries associated with possible lateral/rotational stress. The scenario for such injuries may be associated with tail usage in defense from a predator, affecting the distal tail and causing centrum fractures and joint pathologies due to an increase of flexibility from the proximal to distal part of the tail. Moreover, because hadrosaurs are presumably facultatively bipedal, running on hindlimbs for enhanced speed (perhaps attempting to escape a predator), the distal tail was more vulnerable to injuries due to tail biomechanics and its relationship with muscle and tendon arrangement as previously mentioned.

Due to the nature of our bonebed with scattered, disassociated, and mostly disarticulated bones, it is difficult to determine if the caudal vertebra specimens with trauma belong to a few animals highly injured within the tail region or if they belong to a larger number of animals. However, due to previous reports on the high frequency of trauma in hadrosaur caudal vertebrae (Rothschild and Tanke 1992; Carpenter 1998; Rega 2012; De Palma et al. 2013; Rothschild and Tanke 2014), we conclude that the high frequency of trauma associated with caudal vertebra within our specimens also represents a commonality to tail injuries among hadrosaurs.

CONCLUSIONS

Hadrosaur bone modification with indication of trauma has been previously reported, with implications for behavior. In our study of the *E. annectens*, we likewise observed similar patterns and occurrences. Our findings indicate that pre-mortem trauma was associated with specific body regions. Most of the bone modifications that we associated with trauma or mechanical stress were more frequent in caudal vertebrae. However, occasional examples of trauma in rib, chevron, and phalanx of the manus were also observed, and most likely resulted from occasional accidental injuries rather than the result of patterns of behavior.

The frequency of pre-mortem bone modifications indicative of trauma, and localization of trauma within the tail body region, suggests that individuals of *E. annectens* frequently suffered tail injury during their lifespan. Proximal tail trauma suggests occasional and accidental fractures of mostly neural spines. The proximal tail was stable and less flexible due to the interaction of ossified tendons and muscular arrangement of large hypaxial muscles that biomechanically were important for animal posture, especially when running.

Bone reactions, indicative of mechanical stress or micro-fracture, increase in frequency within the middle to the middle-distal tail regions, relative to proximal region. Most bone modifications in the middle/middle-distal tail region occur in the vertebral neural spines. Bone remodeling indicative of hypertrophic ossification in the neural spines suggests the causative mechanism was initiated by mechanical stress. Because this region lacks ossified tendons and has less massive hypaxial musculature, the architectural rigidity and stability of the tail decreases within the middle tail region, a laxity continuing into the distal tail (Organ 2006; Persons and Currie 2014). Thus, especially during running, the effects of the epaxial muscle pulling on the neural spines on the region is uncountered by ossified ligament stabilization found more proximally, causing the hypertrophic ossification. Also, accidental fractures of neural spines increase because this is a more vulnerable portion of the tail, especially if the animal is using the tail occasionally as a defense mechanism.

In the very distal portion of the tail, osseous architecture is further weakened. The spinous processes are less massive, bearing attachments for less massive investing musculature and ligament. While the distal tail is potentially susceptible to trampling, the pattern of centrum fracture observed may also have been due to injury caused by intervertebral hypermobility. In our study, centrum bone perforations between opposing joint surfaces (indicative of pathology) are only found in the distal tail. Moreover, the fractures observed in this sample are not the comminuted pattern indicative of multiple fracture plains created by crush injury. Rather, the orientation and location of fractures is indicative of mechanical

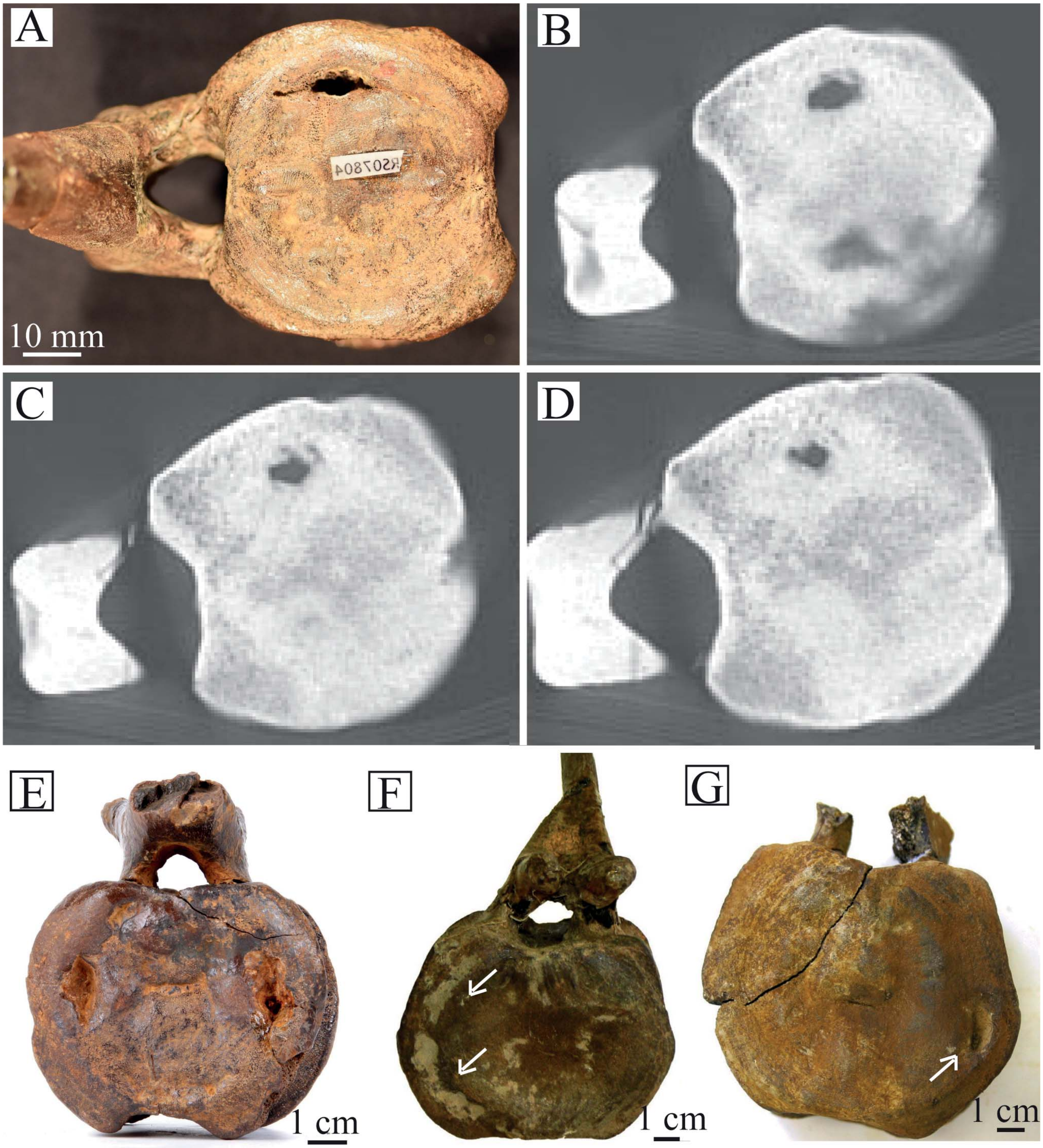

FIG. 13.—Centra with bone perforations/depressions from caudal vertebrae within the distal region of the tail. **A**) Specimen HRS07804 caudal view. **B**–**D**) Sequence of serial CT scan images from caudal (B) to cranial (D). **E**–**G**) Distal caudal vertebrae with perforations similar to 13A: Caudal view of specimen HRS07884 (E); caudal view of specimen HRS04211 (F); caudal view of specimen HRS05808 (G). White arrows point to perforations/depressions.

failure in the centrum, possibly due to a combination of hyperflexion, compression and rotation of tail. Degeneration of the inter vertebral disc or disco-vertebral junction trauma may further impact these fractures (Resnick et al. 1995; Christiansen and Bouxsein 2010) Thus, the inter-joint mobility may be related to the frequency of centrum fractures of the distal tail.

We conclude that the frequent trauma within the tail is correlated with the tail anatomy and biomechanics, and directly associated with the effects of running, tail usage and occasional trampling/bumping.

For future study it is important to continue to analyze and compare other bonebeds and/or more specimens of hadrosaurs for the frequency of pre-mortem trauma and body region association. These findings will continue to shed light into our understanding of hadrosaur biomechanics, behavior and the associated effects recorded on the bones as modifications indicative of trauma, mechanical stress and other pathologies.

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REFERENCES

Aghababian, R.V. and Conte, J.E., 1980, Mammalian bite wounds: Annals of Emergency Medicine, v. 9, p. 79–83.

Antinoff, N., 1997, Osteomyelitis in reptiles: Proceedings Association of Reptilian and Amphibian Veterinarians, v. 4, p. 149–152.

Aslan, A. and Behrensmeyer, A.K., 1996, Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: the East Fork River, Wyoming: PALAIOS, v. 11, p. 411–421.

Barile, A., Limbucci, N., Splendiani, A., Gallucci, M., and Masciocchi, C., 2007, Spinal injury in sport: European Journal of Radiology, v. 62, p. 68–78.

Bell, P.R. and Coria, R.A., 2013, Palaeopathological survey of a population of Mapusaurus (Theropoda: Carcharodontosauridae) from the Late Cretaceous Huincul Formation, Argentina: PloS one, v. 8, e63409.

Campione, N.E., 2014, Postcranial anatomy of *Edmontosaurus regalis* (Hadrosauridae) from the Horseshoe Canyon Formation, Alberta, Canada *in* D.A. Eberth and D.C. Evans (eds.), Hadrosaurs: Indiana University Press, Bloomington, IN, p. 208–244.

Campione, N.E. and Evans, D.C., 2011, Cranial growth and variation in Edmontosaurs (Dinosauria: Hadrosauridae): implications for the latest Cretaceous megaherbivore diversity in North America: PLoS ONE, v. 6, e25186

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

Christiansen, B.A. and Bouxsein, M.L., 2010, Biomechanics of vertebral fractures and the vertebral fracture cascade: Current Osteoporosis Reports, v. 8, p. 198–204.

Cohen, J., 1988, Statistical Power Analysis for the Behavioral Sciences, second edition: Lawrence Erlbaum Associates, Hillsdale, NJ, 567 p.

De Palma, R.A., Burnham, D.A., Martin, L.D., Rothschild, B.M., and Larson, P.L., 2013, Physical evidence of predatory behavior in *Tyrannosaurus rex*: Proceedings of the National Academy of Sciences, v. 110, p. 12560–12564.

De Souza Barbosa, F.H., De Oliveira Porpino, K., and Fragoso, A.B.L., 2013, Osteomyelitis in Quaternary mammal from the Rio Grande do Norte State, Brazil: Quaternary International, v. 299, p. 90–93.

Dumbravă, M.D., Rothschild, B.M., Weishampel, D.B., CSIKI-SAVA, Z., Andrei, R.A., Acheson, K.A., and Codrea, V.A., 2016, A dinosaurian facial deformity and the first occurrence of ameloblastoma in the fossil record: Scientific Reports, v. 6, p. 29271.

Farke, A.A., Wolff, E.D., and Tanke, D.H., 2009, Evidence of combat in Triceratops: PLoS One, v. 4, p. e4252.

Foth, C., Evers, S.W., Pabst, B., Mateus, O., Flisch, A., Patthey, M., and Rauhut, O.W., 2015, New insights into the lifestyle of *Allosaurus* (Dinosauria: Theropoda) based on another specimen with multiple pathologies: PeerJ, v. 3, p. e940.

García, R.A., Cerda, I.A., Heller, M., Rothschild, B.M., and Zurriaguz, V., 2017, The first evidence of osteomyelitis in a sauropod dinosaur: Lethaia, v. 50, p. 227–236.

Hanna, R.R., 2002, Multiple injury and infection in a sub-adult theropod dinosaur *Allosaurus fragilis* with comparisons to allosaur pathology in the Cleveland-Lloyd dinosaur quarry collection: Journal of Vertebrate Paleontology, v. 22, p. 76–90.

Horner, H.R., Weishampel, D.B., and Forster, C.A., 2004, Hadrosauridae, *in* D.B. Weishampel, P. Dodson, and H. Osmolska (eds.), The Dinosauria, second edition: University of California Press, California, p. 438–463.

Hunt, T.C., Peterson, J.E., Frederickson, J.A., Cohen, J.E., and Berry, J.L., 2019, First documented pathologies in Tenonto*saurus tilletti* with comments on infection in non-avian dinosaurs: Scientific Reports, v. 9, p. 1–8.

Montali, R.J., 1988, Comparative pathology of inflammation in higher vertebrates (reptiles, birds and mammals): Journal of Comparative Pathology, v. 99, p. 1–27.

Moodie, R.L., 1918, Studies in paleopathology: general consideration of the evidences of pathological conditions found among fossil animals: Paul B. Hoeber, New York, p. 374–393.

Moran, M.D., 2003, Arguments for rejecting the sequential Bonferroni in ecological studies: Oikos, v. 100, p. 403–405.

Nakagawa, S., 2004, A farewell to Bonferroni: the problems of low statistical power and publication bias: Behavioral Ecology, v. 15, p. 1044–1045.

Organ, C.L., 2006, Biomechanics of ossified tendons in ornithopod dinosaurs: Paleobiology, v. 32, p. 652–665.

McLain, M.A., Nelsen, D., Snyder, K., Griffin, C.T., Siviero, B., Brand, L.R., and Chadwick, A.V., 2018, Tyrannosaur cannibalism: a case of a tooth-traced tyrannosaurid bone in the Lance Formation (Maastrichtian), Wyoming: PALAIOS, v. 33, p. 164–173.

Pathria, M., 1995, Physical injury: spine, *in* D. Resnick and C.F. Fix (eds.), Diagnosis of Bone and Joint Disorders, third edition: W.B. Saunders, Philadelphia, p. 2825–2898.

Paul G.S., 2016, The Princeton field guide to dinosaurs, second edition: Princeton University Press. Princeton, UK, p. 360.

Persons, W.S., IV and Currie, P.J., 2014, Duckbills on the run: the cursorial abilities of hadrosaurs and implications for tyrannosaur-avoidance strategies, *in* D.A. Eberth and D.C. Evans (eds.), Hadrosaurs: Indiana University Press, Bloomington, IN, p. 449–458.

Rega, E., 2012, Disease in dinosaurs, *in* M.K. Brett-Surman, T.R. Holtz, Jr., and J.O. Farlow (eds.), The Complete Dinosaur, second edition: Indiana University Press, Bloomington, IN, p. 667–711.

Rega, E.A. and Brochu, C.A., 2001, Paleopathology of a mature *Tyrannosaurus rex* skeleton: Journal of Vertebrate Paleontology, v. 21, p. 92A.

Rega, E.A., Holmes, R., and Tirabasso, A., 2010, Habitual locomotor behavior inferred from manual pathology in two Late Cretaceous Chasmosaurine Ceratopsid Dinosaurs, *Chasmosaurus Irvinensis* (CMN 41357) and *Chasmosaurus Belli* (ROM 843), *in* M.J. Ryan, B. Chinnery-Allgeier, and D.A. Eberth (eds.), New Perspectives on Horned Dinosaurs: Indiana University Press, Bloomington, p. 340–354.

Reisz, R.R., Scott, D.M., Pynn, B.R., and Modesto, S.P., 2011, Osteomyelitis in a Paleozoic reptile: ancient evidence for bacterial infection and its evolutionary significance: Naturwissenschaften, v. 98, p. 551–555.

Resnick, D., Goergen, T.G., and Niwayama, G., 1995, Physical injury: concepts and terminology, *in* D. Resnick and C.F. Fix (eds.), Diagnosis of Bone and Joint Disorders, third edition: W.B. Saunders, Philadelphia, p. 2561–2692.

Revel, M., Andre-Deshays, C., Roudier, R., Roudier, B., Hamard, G., and Amor, B., 1992, Effects of repetitive strains on vertebral end plates in young rats: Clinical Orthopaedics and Related Research, v. 279, p. 303–309.

Rosthschild, B.M., 1997, Dinosaurian paleopathology, *in* J.O. Farlow and M.K. Brett-Surman (eds.), The Complete Dinosaur, first edition: Indiana University Press, Bloomington, IN, p. 426–448.

Rothschild, B.M. and Tanke, D.H., 1992, PALEOSCENE 13, paleopathology of vertebrates: insights to lifestyle and health in the geological record: Geoscience Canada, v. 19, p. 79–82.

Rothschild, B.M. and Tanke, D.H., 2007, Osteochondrosis in Late Cretaceous Hadrosauria: a manifestation of ontologic failure *in* K. Carpenter (ed.), Horns and Beaks: Ceratopsian and Ornithopod Dinosaurs: Indiana University Press, Bloomington, p. 171–183.

Siviero, B., Brand, L., and Chadwick A., 2016, Bone modifications indicating pathology within a monospecific hadrosaur bonebed from the Lance Formation (Maastrichtian), Wyoming: Society of Vertebrate Paleontology Annual Meeting Salt Lake City, UT: Abstracts with Programs 2016, p. 225.

Tanke, D.H., 1989, K/U centrosaurine (Ornithischia: Ceratopsidae) paleopathologies and behavioral implications: Journal of Vertebrate Paleontology, v. 9, p. 41A.

Tanke, D.H. and Currie, P.J., 1998, Head-biting behavior in theropod dinosaurs: paleopathological evidence: Gaia, v. 15, p. 167–184.

Tanke, D.H. and Farke, A.A., 2006, Bone resorption, bone lesions, and extracranial fenestrae in ceratopsid dinosaurs: a preliminary assessment, *in* K. Carpenter (ed.), Horns and Beaks: Ceratopsian and Ornithopod Dinosaurs: Indiana University Press, Bloomington, p. 319–347.

Tanke, D.H. and Rothschild, B.M., 2010, Paleopathologies in Albertan ceratopsids and their behavioral significance *in* M.J. Ryan, B. Chinnery-Allgeier, and D.A. Eberth (eds.), New Perspectives on Horned Dinosaurs: Indiana University Press, p. 355–384.

TANKE, D.H. AND ROTHSCHILD, B.M., 2014, Paleopathology in Late Cretaceous Hadrosauridae from Alberta, Canada, *in* D.A. Eberth and D.C. Evans (eds.), Hadrosaurs: Indiana University Press, Bloomington, IN, p. 540–571.

TELL, L.A., FERRELL, S.T., AND GIBBONS, P.M., 2004, Avian mycobacteriosis in free-living raptors in California: 6 cases (1997–2001): Journal of Avian Medicine and Surgery, v. 18, p. 30–40.

TULLY JR, T.N., MARTIN, G.S., HAYNES, P.F., CORNICK-SEAHORN, J., AND PECHMAN, R.D., JR., 1996, Tarsometatarsal sequestration in an Emu (*Dromaius novaehollandiae*) and an Ostrich (*Struthio camelus*): Journal of Zoo and Wildlife Medicine, v. 27, p. 550–556.

ULLMANN, P.V., SHAW, A., NELLERMOE, R., AND LACOVARA, K.J., 2017, Taphonomy of the Standing Rock hadrosaur site, Corson County, South Dakota: PALAIOS, v. 32, p.779–796.

VOORHIES, M.R., 1969, Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska: Contributions to Geology, v. 1, p. 1–69.

XING H., MALLON J.C., AND CURRIE M.L., 2017, Supplementary cranial description of the types of *Edmontosaurus regalis* (Ornithischia: Hadrosauridae), with comments on the phylogenetics and biogeography of Hadrosaurinae: PLoS ONE, v. 12, e0175253, doi.org/10.1371/journal.pone.0175253.

XING, L., ROTHSCHILD, B.M., RANDOLPH-QUINNEY, P.S., WANG, Y., PARKINSON, A.H., AND RAN, H., 2018, Possible bit-induced abscess and osteomyelitis in *Lufengosaurus* (Dinosauria: sauropodomorph) from Lower Jurassic of the Yimen Basin, China: Scientific Reports, v. 8, p. 5045.

WOLFF, E.D., SALISBURY, S.W., HORNER, J.R., AND VARRICCHIO, D.J., 2009, Common avian infection plagued the tyrant dinosaurs: PLoS One, v. 4, p. el7288.

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