




# A partial tyrannosauroid femur from the mid-Cretaceous Wayan Formation of eastern Idaho, USA

L. J. Krumenacker,<sup>1,2,3</sup>  Lindsay E. Zanno<sup>4,5\*</sup>  and Hans-Dieter Sues<sup>6</sup> 

<sup>1</sup>Department of Geosciences, Idaho State University, Pocatello, Idaho, 83209, USA <[krumlaur@isu.edu](mailto:krumlaur@isu.edu)>

<sup>2</sup>Department of Physical Sciences, College of Eastern Idaho, Idaho Falls, Idaho, 83404, USA <[lj.krumenacker@cei.edu](mailto:lj.krumenacker@cei.edu)>

<sup>3</sup>Science Department, Mountain View Middle School, Blackfoot, Idaho, 83221, USA. <[krumlaur@d55.k12.id.us](mailto:krumlaur@d55.k12.id.us)>

<sup>4</sup>Paleontology, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, 27601, USA <[lindsay.zanno@naturalsciences.org](mailto:lindsay.zanno@naturalsciences.org)>

<sup>5</sup>Department of Biological Sciences, North Carolina State University, Raleigh, North Carolina, 27695, USA

<sup>6</sup>Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, MRC 121, P.O. Box 37012, Washington, DC 20013-7012, USA <[suesh@si.edu](mailto:suesh@si.edu)>

**Abstract.**—The diversity of mid-Cretaceous tyrannosauroids is poorly understood. We describe a partial tyrannosauroid femur from the Albian–Cenomanian Wayan Formation of eastern Idaho that helps to fill in an important spatiotemporal gap in the North American record of tyrannosaurs. This specimen, consisting of the proximal half of the bone, is morphologically similar to the femur of *Moros intrepidus*, a small-bodied tyrannosauroid from the Cenomanian Mussentuchit Member of the Cedar Mountain Formation of Utah, but not referable to this taxon. The Wayan femur lacks an autapomorphy diagnostic for *Moros intrepidus*, indicating the presence of a previously unrecognized tyrannosauroid taxon in the early Late Cretaceous of Laramidia. Histological results indicate that, at the time of death, this individual was at least five years old, skeletally immature, and undergoing growth at a moderate rate. The addition of this tyrannosauroid to the Wayan–Vaughn Assemblage provides additional evidence for the widespread distribution of various tyrannosauroid taxa in Laramidia during the early Late Cretaceous.

## Introduction

Although Campanian and Maastrichtian terrestrial vertebrate assemblages of North America are among the best understood and best sampled for dinosaurs worldwide, early Late Cretaceous (Cenomanian–Turonian) assemblages, are still poorly known. Theropod dinosaurs from this time interval are particularly poorly represented by fossils. Key among these are tyrannosaurids, the well-studied apex predators of the Late Cretaceous, typified by *Tyrannosaurus rex* Osborn, 1905. Evidence for the origin of tyrannosaurids and their replacement of allosauroids as the apex predators in Late Cretaceous ecosystems, is still scant. To date, the record consists of the fragmentary hindlimb of *Moros intrepidus* Zanno et al., 2019, and isolated tyrannosauroid teeth from the Cenomanian Mussentuchit Member of the Cedar Mountain Formation of Utah (Zanno and Makovicky, 2013; Zanno et al., 2019), partial skeletons of the Turonian-age *Suskityrannus hazelae* Nesbitt et al., 2019, from the Moreno Hill Formation of New Mexico (Nesbitt et al., 2019), isolated tyrannosauroid teeth from the Albian–Cenomanian Wayan Formation of Idaho (Krumenacker et al., 2016), and somewhat older isolated tyrannosauroid teeth from the Aptian–Albian Cloverly Formation of Wyoming (Zanno and Makovicky, 2011). Together, these discoveries indicate the

presence of several morphologically similar tyrannosauroids in the late Early through early Late Cretaceous of North America (Zanno and Makovicky, 2011).

The addition of *Moros intrepidus* and *Suskityrannus hazelae*, as well as the more paleogeographically distant *Timurlengia euotica* Brusatte et al., 2016, from the Turonian-age Bissekty Formation of Uzbekistan (Brusatte et al., 2016), have narrowed the wide gaps in the fossil record of tyrannosauroids during the early Late Cretaceous, before tyrannosaurids assumed the role of apex predators. However, these taxa come from widely separated paleogeographic areas and temporal intervals, leaving significant gaps and making any additional data valuable to enhance our understanding of tyrannosauroid evolution and paleobiogeography.

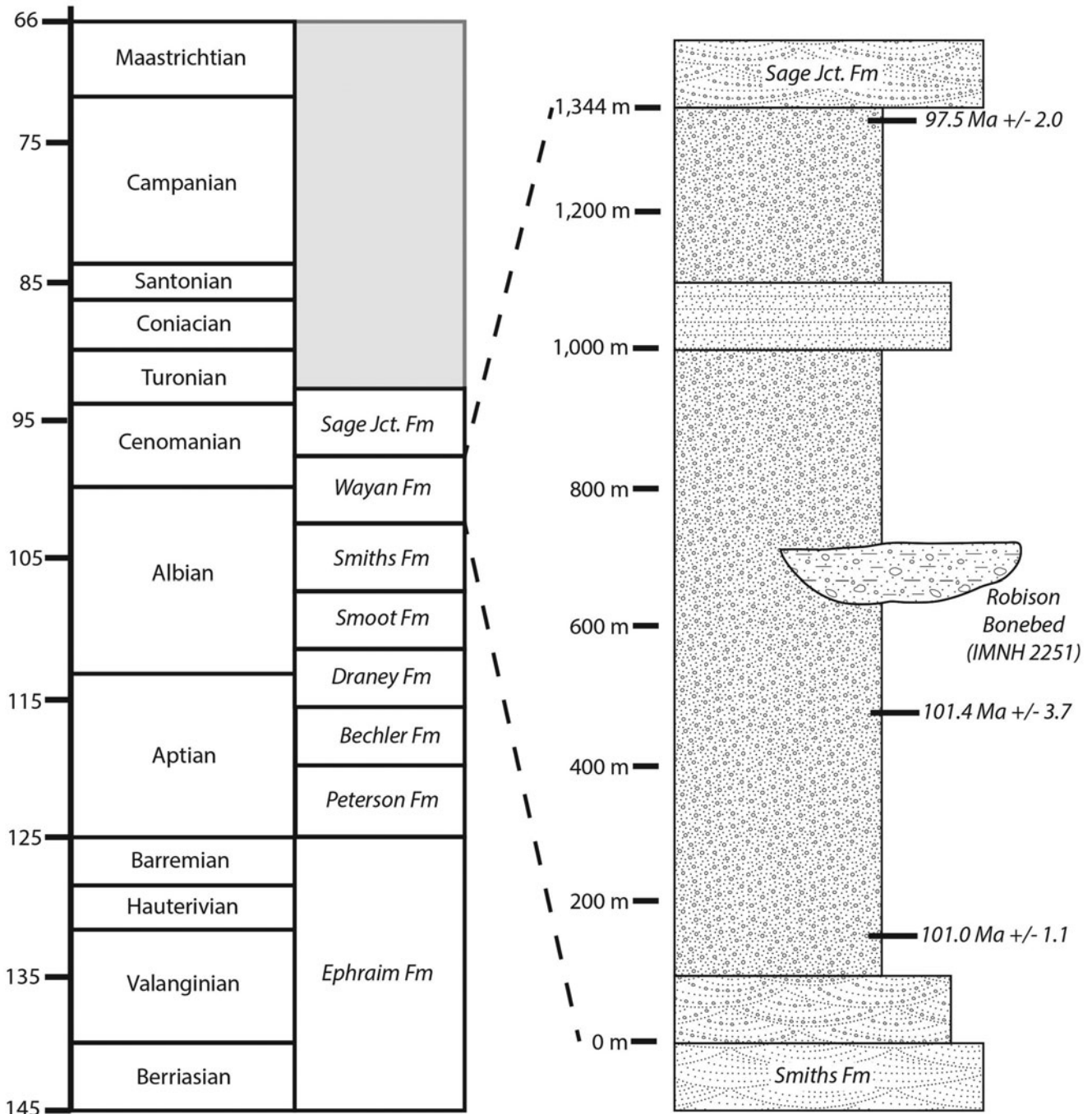
The late Albian–Cenomanian Wayan–Vaughn Assemblage (hereafter referred to as the WVA) of southeastern Idaho and southwestern Montana is the northernmost reported North American early Late Cretaceous dinosaurian assemblage known from skeletal remains to date. Here we add to the growing body of data concerning mid-Cretaceous North American tyrannosauroids, and the composition of the WVA, by describing the morphology and histology of a partial tyrannosauroid femur from the Wayan Formation and exploring its implications.

## Geological setting

The fossil described here was collected from the Robison Bonebed in eastern Bonneville County, Idaho (Figs. 1, 2). The

‡Authors contributed equally.

\*Corresponding author.

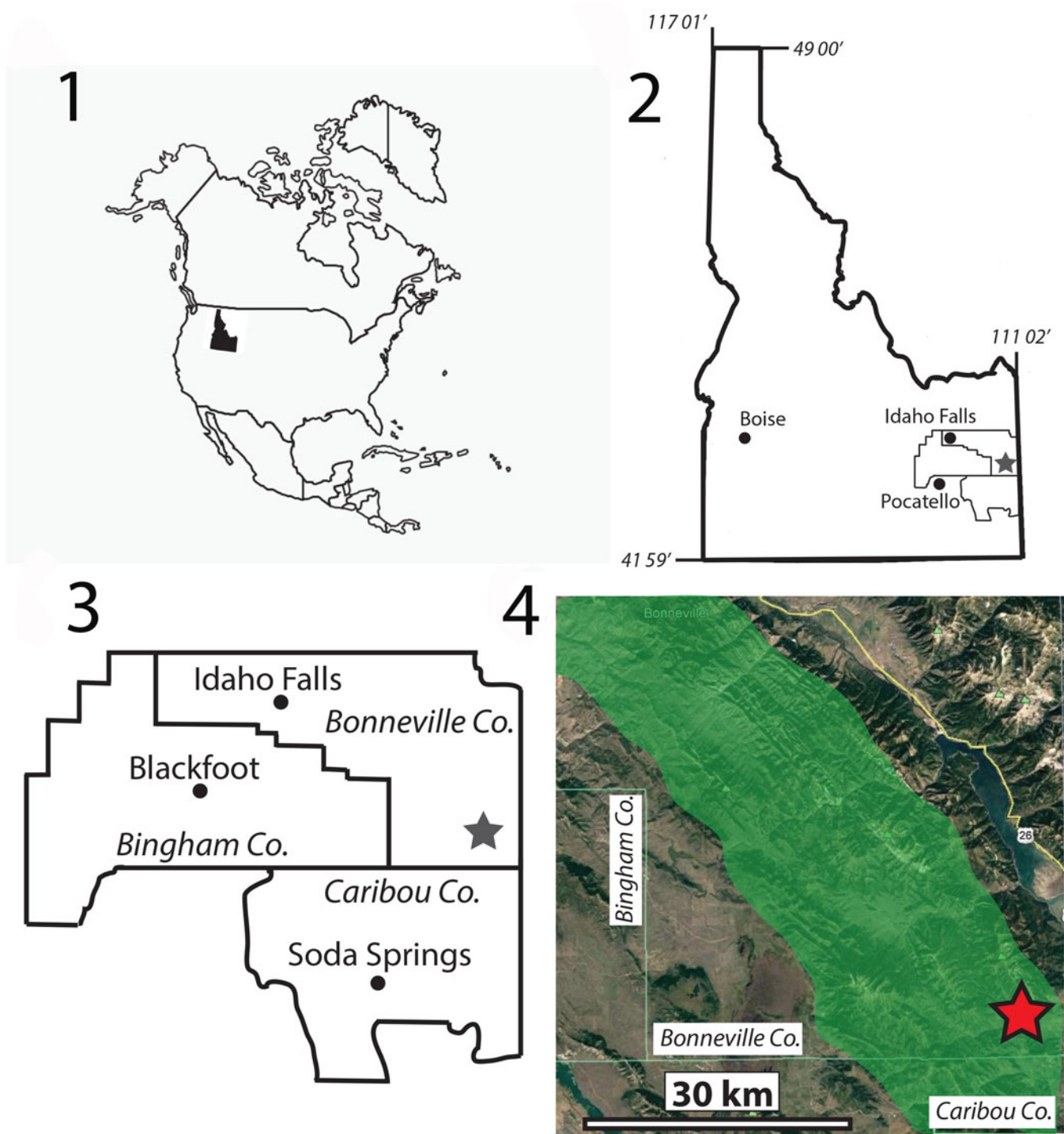


**Figure 1.** Stratigraphy of the study area. Cretaceous formations, including the Wayan Formation, of the Caribou Range of southeastern Idaho; Sage Jct. Fm = Sage Junction Formation. The approximate stratigraphic interval of the Robison Bonebed is shown, as well as radiometric dates recovered from certain stratigraphic horizons (data from Dorr, 1985; Krumenacker, 2010; Krumenacker et al., 2016; Ross et al., 2017).

Robison Bonebed is the most productive vertebrate fossil locality known to date from the Wayan Formation (Krumenacker et al., 2014) and has produced skeletal remains of numerous taxa, including diverse theropods (Krumenacker et al., 2016), ankylosaurs, iguanodontians, the neornithischian *Oryctodromeus cubicularis* Varricchio, Martin, and Katsura, 2007 (Krumenacker, 2019; Krumenacker et al., 2019), mammals, crocodyliforms, turtles, and fishes (Krumenacker et al., 2014). Fossils from this location include mostly isolated elements that exhibit taphonomic

alteration, including broken and worn ends and varying degrees of abrasion (Krumenacker et al., 2016; Krumenacker et al., 2019). Combined sedimentological and taphonomic evidence suggests the Robison Bonebed represents a short-lived debris-flow depositional setting (Krumenacker et al., 2016).

The Wayan Formation dominantly consists of poorly exposed variegated mudstones and siltstones, with subordinate coarse-grained lithologies such as those of the Robison Bonebed (Dorr, 1985; Weishampel et al., 2002; Krumenacker, 2010, 2017).



**Figure 2.** Geographic location of study. Location of Idaho in the continental United States (1), Bingham, Bonneville, and Caribou counties where the Wayan Formation crops out (2, 3), and location of Cretaceous outcrops in Bonneville and Caribou counties (4) with location of Robison Bonebed (star).

Deposition occurred associated with a meandering fluvial system adjacent to highlands of the Sevier Thrust Belt to the west and the Mowry Seaway to the east (Schmitt and Moran, 1982; Dorr, 1985; Krumenacker, 2010). Outcrops are limited to the Caribou Range and adjacent areas of Bonneville and Caribou counties, Idaho (Fig. 2.2–2.4). Attaining a thickness of 1344 m in the Tincup Canyon area of Caribou County, the Wayan Formation transitions into three formations (the Thomas Fork, Cokeville, and Quealy

formations) in the thrust belt of western Wyoming (Rubey, 1973). The Wayan Formation is slightly older than the Mussentuchit Member of the Cedar Mountain Formation in central Utah and the geographically proximate Vaughn Member of the Blackleaf Formation in western Montana (Krumenacker, 2019; Tucker et al., 2020).

Recognition of the WVA is based on the distinct paleontological similarities shared with the Vaughn Member of the



Blackleaf Formation of Montana but not with the Mussentuchit Member of the Cedar Mountain Formation (Krumenacker, 2019). The WVA exhibits a relative abundance of skeletal remains of the burrowing orodromine neornithischian *Oryctodromeus cubicularis*, as well as eggshell fragments and rare eggs assigned to the ootaxon *Macroelongatoolithus carleylei* Zelenitsky, Carpenter, and Currie, 2000, which indicates the presence of large oviraptorosaurs (Krumenacker et al., 2016). Other vertebrates are much less common and known only from isolated and fragmentary remains. These include the taxa described for the Robison Bonebed above, as well as the cimolodontian multituberculate *Cimolodon akersteni* Weaver et al., 2019, and other mammals (Weaver et al., 2019). Additionally, unidentified freshwater mollusks and a limited florule, including the ferns *Gleichenia* sp., *Anemia* sp., and *Geinitzia* sp., are known from Wayan outcrops (Krumenacker, 2019).

## Materials and methods

**Paleosteohistology.**—We removed a 1×2 cm sized cortical fragment from the distalmost margin of the medial side of the femoral shaft along original cracks for histological sampling using standardized techniques (Lamm, 2013). Although originating from the medial shaft, this region was the closest to the mid-diaphysis as possible, and thus most likely to preserve a complete growth record (Padian et al., 2013). This fragment was embedded in a clear epoxy resin (EPO-TEK 301), sectioned transversely (Buehler IsoMet 1000 Precision Saw), and polished on one side (Buehler MetaServ 250 Grinder Polisher) using abrasive paper disks of 400–1200 grit sizes. Polished blocks were affixed to glass slides with epoxy and ground to a thickness of ~100–80 μm. Petrographic sections were observed with a Nikon Eclipse Ci POL microscope equipped with a polarizer and a lambda filter and imaged with a Nikon DS-Fi2 digital camera.

**Repository and institutional abbreviations.**—Idaho Museum of Natural History (IMNH), Idaho State University, Pocatello, Idaho; Arizona Museum of Natural History (MSM), Mesa, Arizona; North Carolina Museum of Natural Sciences (NCSM), Raleigh, North Carolina.

## Systematic paleontology

Dinosauria Owen, 1842  
 Theropoda Marsh, 1881  
 Coelurosauria Huene, 1914  
 Tyrannosauroida Osborn, 1905  
 Genus and species indet.

Figures 3, 4

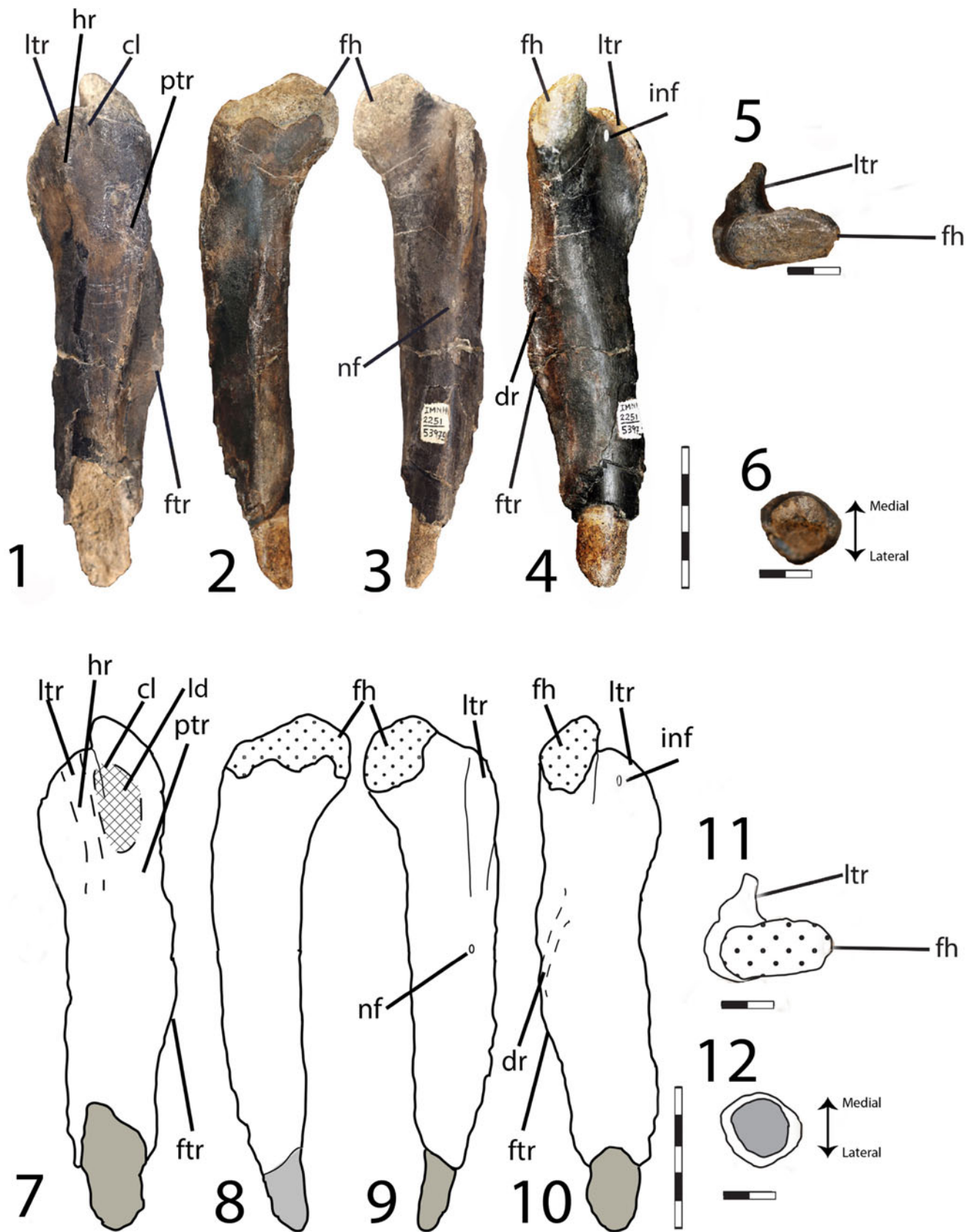
**Occurrence.**—Robison Bonebed, Bonneville County, Idaho, USA. Wayan Formation. Late Early to early Late Cretaceous (Albian–Cenomanian).

**Description and comparisons.**—The preserved portion of the femur indicates an anteriorly bowed shaft (Fig. 3.1, 3.4) as in *Moros intrepidus* (Fig. 5.1, 5.4), but in contrast to *Suskityrannus hazelae*, which has a straighter femoral shaft

(MSM P6178). The proximal end of the femoral shaft is suboval in cross-section (Fig. 3.5) and broader anteroposteriorly than mediolaterally, as in *Moros intrepidus* and *Suskityrannus hazelae* (MSM P6178). The femoral head is dorsally inclined as in tyrannosauroids generally (Fig. 3.2, 3.3) and appears to exhibit a more extreme inclination than that of *Suskityrannus* (Nesbitt et al., 2019). However, the exact orientation and morphology of the greater trochanter and femoral head cannot be determined due to poor preservation of the proximal end. The ventral margin of the femoral head on IMNH 2251/53975 slopes gently dorsomedially from the femoral shaft (Fig. 3.3), in contrast to that of *Suskityrannus hazelae* (MSM P6178), in which it angles sharply medially.

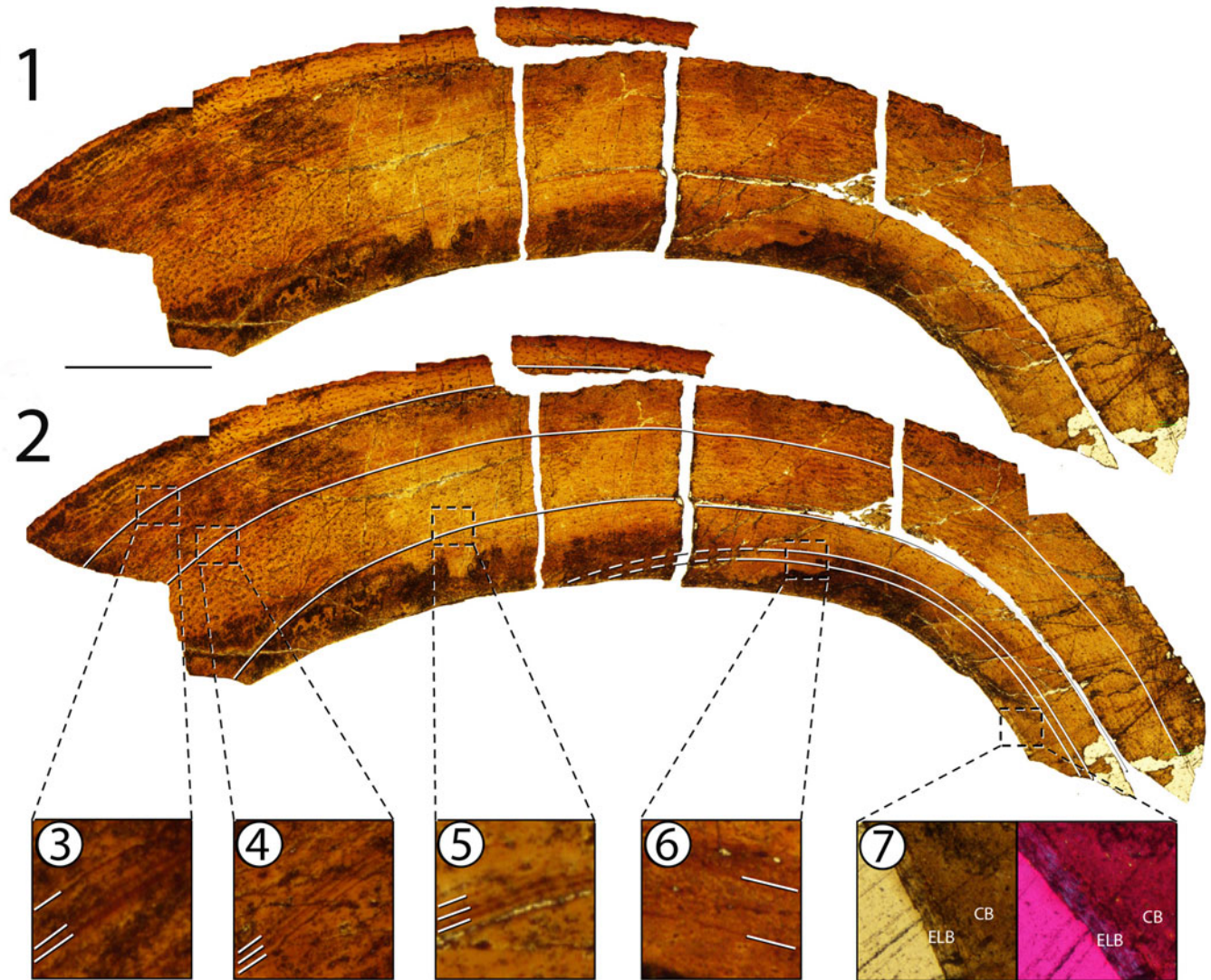
The lesser trochanter forms a prominent alariform crest (Fig. 3.1, 3.4) as in *Guanlong wucuii* Xu et al., 2006, and *Dilong paradoxus* Xu et al., 2004. It is oriented slightly anteromedial to the axis of the femoral head, as in *Moros intrepidus* and *Suskityrannus hazelae*, but less so than in tyrannosaurids (Zanno et al., 2019). There is a distinct sinuosity to the lesser trochanter (Fig. 3.3), whereby the proximalmost aspect is medially concave and the distalmost aspect is laterally concave. A similar morphology is observed on *Suskityrannus hazelae* (MSM P6178); however, this region is poorly preserved in *Moros intrepidus* (Fig. 5, NCSM 33392). The lesser trochanter terminates at approximately the level of the greater trochanter, or slightly distal to that, and is tightly appressed to the greater trochanter, separated by only a shallow, narrow cleft, as in tyrannosauroids generally (Fig. 3.1, 3.4) and unlike the condition in ornithomimosauroids, which possess a wide intertrochanteric space and a lesser trochanter that terminates well distal to the greater trochanter (Makovicky et al., 2004). Due to damage, it cannot be determined whether an accessory trochanter was present. IMNH 2251/53975 lacks the semicircular tuberosity near the lesser trochanter that is autapomorphic for *Moros intrepidus* (Zanno et al., 2019; Fig. 5.1). A lateral depression bounded anteriorly by a hypertrophied proximodistal ridge on the lateral aspect of the lesser trochanter and posteriorly by a bulbous posterior trochanter (Fig. 3.1) is present on IMNH 2251/53975, as in *Moros intrepidus*, *Suskityrannus hazelae* (MSM P6178), other tyrannosauroids, and ornithomimosauroids (Zanno et al., 2019). Among ornithomimosauroids, this condition is similar to that observed on ROM 852, but not well developed on other taxa. A single intertrochanteric nutrient foramen (sensu Zanno et al., 2019) is present (Fig. 3.4) on the lesser trochanter close to its proximalmost margin, as in some tyrannosauroids and ornithomimosauroids (Zanno et al., 2019). A large nutrient foramen is also present distal to the lesser trochanter (Fig. 3.3); it is located only slightly medial to the axis of the lesser trochanter, as in *Teratophonus curriei* Carr et al., 2011 (UMNH VP 16690), and less medially oriented than *Moros intrepidus* (Fig. 5.3).

The fourth trochanter forms a proximodistally long, mediolaterally thick crest (Fig. 3.1, 3.4), which bounds the concave posterolateral surface of the femoral shaft. It appears to be slightly bilobate, as in *Moros intrepidus* (Fig. 5; Zanno et al., 2019) and *Suskityrannus hazelae* (MSM P6178). In those two taxa, the distal lobe is larger, whereas both lobes appear similar in their posterior extent in IMNH 2251/53975. The fourth trochanter is located on the posteromedial surface of the shaft. Yet it is less medially oriented than in tyrannosauroids, including *Xiongguanlong baimoensis* Li et al., 2009,



**Figure 3.** IMNH 2251/53975, partial left tyrannosauroid femur, actual specimen (1–6) and interpretive drawings (7–12), in lateral (1), posterior (2), anterior (3), medial (4), proximal (5), and distal (6) views. Abbreviations: cl, cleft between greater and lesser trochanter; dr, dorsomedial ridge; fh, femoral head; ftr, fourth trochanter; hr, hypertrophied proximodistal ridge; inf, intertrochanteric nutrient foramen (lightened electronically for visibility); ld, lateral depression; ltr, lesser trochanter; nf, nutrient foramen; and ptr, posterior trochanter. Scale bars (1–4) 5 cm and (5, 6) 2 cm. Stippled areas on interpretive drawing represent broken and eroded portions, shaded areas indicate matrix infill, and the crosshatched area indicates the lateral depression (ld). Scale bars marked in centimeters.





**Figure 4.** Partial mid-diaphyseal cross-section of IMNH 2251/53975 shown in polarized light (1) and with four growth markers traced in white lines indicating five growth cycles (2). Growth markers obliterated by Wedl tunnels approximated with dashed lines. Magnification of double and triple lines of arrested growth (LAGs) shown in (3–6). Boundary between endosteal lamellar bone (ELB) and compact cortical bone (CB) shown in polarized and polarized with lambda filter (7). Scale bars (1, 2) 25 mm; (3–7) not to scale.

*Gorgosaurus libratus* Lanbe, 1914, *Moros intrepidus* (Zanno et al., 2019), *Teratophoneus curriei* (UMNH VP 16690), and *Suskityrannus hazelae* (MSM P6178), as well as in ornithomimids (Zanno et al., 2019), where it extends from the medialmost aspect of the posterior surface of the shaft.

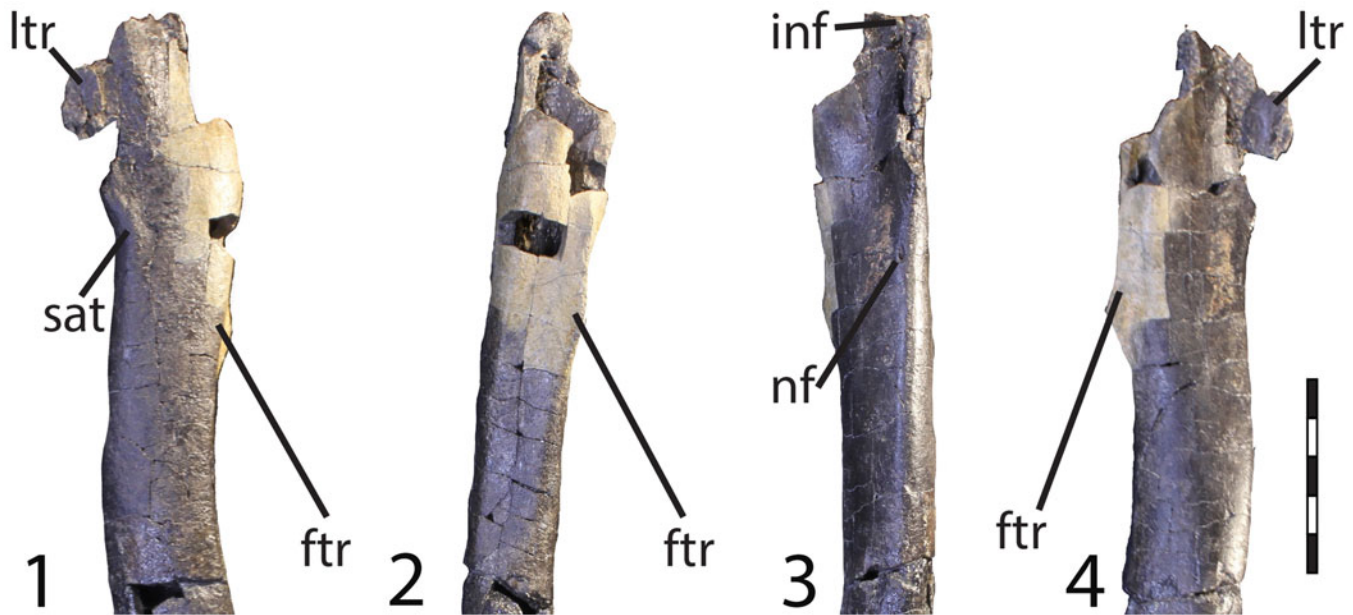
**Remarks.**—IMNH 2251/53975 consists of the proximal half of a left femur (Fig. 3) referable to an indeterminate tyrannosauroid. It is well preserved with minor damage to the femoral head and the lesser and greater trochanters. There is a fresh break distal to the fourth trochanter with a cast of a portion of the medullary cavity preserved in sandstone.

## Results

**Histological results.**—We processed histological ground sections from an anteromedial fragment of the midshaft of

IMNH 2251/53975 to assess relative growth rate and skeletal maturity (Fig. 4). The cortex is thin (~4.8 mm) and poorly preserved. The periosteal and endosteal surfaces exhibit minor erosion, resulting in undulating margins that do not conform to the primary bone microstructure (Fig. 4.1, 4.2). There is extensive degradation from microbial invasion throughout the cortex, including Wedl tunnels (Trueman and Martill, 2002). The presence of Wedl tunnels indicates bacterial bioerosion (Turner-Walker, 2019; Eriksen et al., 2020) and may be linked to wetting and drying cycles and/or modifications of dissolved oxygen levels in soils (Turner-Walker, 2019). Pre-depositional erosion of the endosteal surface cannot have been extensive because a thin layer of lamellar bone lining the medullary cavity is still preserved (Fig. 4.7).

The cortex is zonal and composed exclusively of primary tissue with no apparent evidence of remodeling. Four packages of doublet and triplet lines of arrested growth (LAGs) are visible



**Figure 5.** NCSM 33392, partial right femur of *Moros intrepidus* in lateral (1), posterior (2), anterior (3), and medial (4) views. Original images have been horizontally reversed to facilitate comparison with IMNH 2251/53975. Abbreviations: ftr, fourth trochanter; inf, intertrochanteric nutrient foramen; ltr, lesser trochanter; nf, nutrient foramen; and sat, semicircular accessory tuberosity. Scale bar is 5 cm.

(Fig. 4.2). The growth marker nearest the medullary cavity is composed of a tight LAG doublet as well as two additional, more widely separated LAGs (Fig. 4.6). The remaining growth markers are composed of triplet LAGs (Fig. 4.3, 4.5). In between some of these LAG triplets, faint annuli are observed. We identify these doublet and triplet LAGs as corresponding to single growth events (Castanet et al., 1993), and thus count five annual growth cycles within the cortex. The intervening tissue is relatively homogenous, composed entirely of a parallel-fibered bone matrix pierced by longitudinal simple canals connected by scattered Volkmann's canals. Neither a noticeable change in vascularization nor matrix type is observed toward the periphery, and there is no evidence of an external fundamental system. We did not observe consistently decreasing spacing between growth cycles, which would indicate a slowing growth rate (Fig. 4.2); however, the presence of endosteal lamellar bone indicates that the medullary cavity had ceased to expand at the time of death. In sum, histological indicators suggest the femur belonged to a skeletally immature individual, at least five years old at the time of death and with a moderate growth rate.

## Discussion

*Referral to Tyrannosauroidae.*—IMNH 2251/53975 is incomplete, but preserves sufficient morphological detail for a taxonomic referral. The alariform lesser trochanter, the cleft separating the lesser and greater trochanters, and the ridge-like fourth trochanter (Fig. 3) support referral to Tetanurae (Gauthier, 1986). Discrete greater and lesser trochanters divided by a deep cleft (Fig. 3.1) rule out referral to oviraptorosaurians, which either have fused trochanters (e.g., *Anzu wyliei* Lamanna et al., 2014; *Anomalipes zhaoi* Yu et al., 2018; *Oksoko avarsan* Funston et al., 2020) or trochanters separated by a furrow (e.g., *Nankangia jiangxiensis*

Lü et al., 2013), and to dromaeosaurids, which lack a deep notch between the greater and lesser trochanter, except in *Utahraptor ostrommaysi* Kirkland, Burge, and Gaston, 1993 (Turner et al., 2012). Additional evidence against dromaeosaurid affinities for IMNH 53975 is the presence of a ridge-like fourth trochanter (Fig. 3.1, 3.4), which is poorly developed in dromaeosaurids except in *Velociraptor mongoliensis* (Norell and Makovicky, 1999).

Features of IMNH 2251/53975 that are shared with ornithomimosaurs and tyrannosauroids include a lesser trochanter that rises directly from the most pointed apex of the anterior surface of the femoral shaft (Fig. 3.1, 3.4); a fourth trochanter that reaches the base of the lesser trochanter (Fig. 3.1, 3.4); intertrochanteric and principal nutrient foramina (Fig. 3.3, 3.4); a proximal portion of the femur that is depressed lateral to the lesser trochanter and bound distally by a trochanteric shelf; a concave caudal aspect of the femoral shaft (Fig. 3.1); and a femoral shaft that is anteroposteriorly wider in cross-section and anteriorly bowed. Additional features of IMNH 53975 are highly variable in their presence and development among tyrannosauroids and ornithomimosaurs.

On IMNH 2251/53975, the long axis of the lesser trochanter is only slightly anteromedial to the long axis of the femoral head and greater trochanter. This is similar to the condition in *Moros intrepidus* and *Suskityrannus hazelae*, but differs from the condition in *Gorgosaurus libratus* (ROM 1247), *Teratophoneus curriei* (UMNH VP 16690), and *Tyrannosaurus rex* (FMNH PR 2081), in which the lesser trochanter is strongly anteromedially oriented. A strongly anteromedially oriented lesser trochanter is also present in some ornithomimosaurs (ROM 797); however, this is largely the result of a more extensive trochanteric wing that continues to curve medially, and therefore the condition is somewhat different. In addition, the



femoral head of IMNH 2251/53975 is dorsally elevated as in some tyrannosaurs and ornithomimosaurids. However, this feature is variably developed in these clades. For example, the femoral head of some tyrannosauroids (e.g., *Teratophoneus curriei* [UMNH VP 16690] and *Tyrannosaurus rex* [FMNH PR 2081]) is more horizontal, the condition is intermediate in *Suskityrannus hazelae* (Nesbitt et al., 2019), and appears strongly developed in IMNH 2251/53975 and the ornithomimid *Dromiceiomimus brevitertius* (ROM 797).

Despite some general similarities between IMNH 2251/53975 and tyrannosauroid and ornithomimosaurian femora, the former group can be distinguished from the latter based primarily on the morphology of the lesser trochanter. This includes the tight association between the lesser trochanter and greater trochanter/femoral head complex (Fig. 3) that, in IMNH 2251/53975, are separated by a shallow and narrow cleft (Fig. 3.1). This contrasts with the condition in ornithomimids, in which the cleft between the lesser and greater trochanters is distally extensive and the lesser trochanter extends anteriorly on an expanded “neck,” creating a deep and wide space between the femoral head and the lesser trochanter (Makovicky et al., 2004). The lesser trochanter itself is moderately developed, almost semicircular, and extends proximally to the level of the greater trochanter (Fig. 3.1, 3.3, 3.4), which is in contrast to the ornithomimid condition, where the lesser trochanter is more anteriorly extensive in lateral view, rises more steeply along the distal margin from the femoral shaft, and terminates well distal to the greater trochanter. Although the absences of these features can be used to rule out a referral to ornithomimosaurids, they are synplesiomorphic and cannot be used for definite referral of the femur to Tyrannosauroida.

Tyrannosauroid synapomorphies present on the Wayan femur include: (1) location of the principal nutrient foramen on the proximal femoral shaft, which is positioned medial to the axis of the lesser trochanter in tyrannosauroids (Zanno et al., 2019; Fig. 3.3); (2) a proximodistally elongate and bilobate fourth trochanter (Fig. 3.1, 3.4) only observed in *Moros intrepidus* and *Suskityrannus hazelae* to date; and (3) a hypertrophied proximodistal ridge (Fig. 3.1) located on the posterior aspect of the lateral lesser trochanter and resulting in an angular trochanter (this pronounced angulation is absent in ornithomimids), with a convex lateral aspect in proximal view.

There are two unique features in the posterior trochanter of IMNH 2251/53975 that, to our knowledge, have not been reported in other tyrannosaurs: (1) relatively symmetrical lobes of the bilobate posterior trochanter (Fig. 3.1), which is unlike *Moros intrepidus* (Fig. 5) and *Suskityrannus hazelae*, both of which have more extensive distal lobes that, in contrast to tyrannosauroids, exhibit a subtriangular fourth trochanter; and (2) a dorsomedially trending ridge (Fig. 3.4) extending off the proximomedial aspect of the fourth trochanter. Because there is some damage to the proximal end of the fourth trochanter on IMNH 2251/53975 and the rugosity on the fourth trochanter may be intraspecifically variable, we do not deem these features sufficient to name a new taxon.

**Growth and body size.**—Osteohistological features of IMNH 2251/53975 compare well to those of *Moros intrepidus* (Zanno et al., 2019) in that both bear evidence of at least

doublet and triplet LAGs and a moderate growth rate, as evinced by parallel-fibered bone matrix with simple longitudinal canals. Longitudinal canals are also known in *Suskityrannus hazelae*, although reticular canals are also reported along with rarer circumferential vascularity (Nesbitt et al., 2019). *Moros intrepidus*, the Wayan femur, and *Suskityrannus hazelae* (MSM P6178) all represent small to perhaps medium-bodied, skeletally immature individuals aged at least seven, five, and four years, respectively, at the time of death. Whereas *Moros intrepidus* shows decreasing thickness of growth cycles indicating a slowing of growth, it is difficult to identify any consistency in decreasing growth within the femoral fragment sampled for the Wayan tyrannosauroid specimen.

The methods of Campione et al. (2014) were used to estimate the mass of the Wayan taxon using a 92 mm measurement of the shaft circumference taken directly below the fourth trochanter. This suggests a mass of 51 kg, with a likely range between 64–38 kg, and a total possible range between 95–28 kg. The 51 kg mass is roughly one-third less than that of *Moros intrepidus*, which was estimated at 78 kg (Zanno et al., 2019). This lower mass suggests a total femoral length less than the estimated total femoral length of 355 mm for *Moros intrepidus* (Zanno et al., 2019).

**Implications.**—North American early Late Cretaceous tyrannosauroids identifiable at the species level currently only comprise *Moros intrepidus*, from the Cenomanian Mussentuchit Member of the Cedar Mountain Formation of Utah (Zanno et al., 2019), and *Suskityrannus hazelae*, from the Turonian Moreno Hill Formation of New Mexico (Nesbitt et al., 2019). Although fragmentary, the description of the Wayan specimen adds to a growing dataset that is helping to fill gaps in the knowledge concerning tyrannosauroid diversification, distribution, and evolution prior to the emergence of larger-bodied tyrannosauroids of the later Late Cretaceous.

Zanno and Makovicky (2011) described the earliest evidence known for Cretaceous North American tyrannosauroids based on an isolated premaxillary tooth, nearly 1 cm in crown height, from the Aptian–Albian Cloverly Formation of Wyoming. Additional tyrannosauroid premaxillary teeth of similar size (>1 cm crown height) have been reported from the Mussentuchit Member of the Cedar Mountain Formation (Zanno et al., 2019) and the Wayan Formation (Krumenacker et al., 2016).

The Wayan Formation tyrannosauroid is latest Albian–Cenomanian in age (Krumenacker et al., 2016; Krumenacker, 2019). Radiometric dates obtained for the Wayan Formation have a large margin of error, with the top of the formation dating at  $97.5 \pm 2$  Ma, and the middle portion dating at  $99.1 + 1.5/- 1.3$  Ma (Krumenacker, 2010, 2019). Although the Robison Bonebed, due to structural complexities in the outcrop area, cannot be placed in an exact stratigraphic context, it appears to be located within the middle of the Wayan Formation (Krumenacker et al., 2016). *Moros intrepidus*, from the roughly coeval Cenomanian Mussentuchit Member of the Cedar Mountain Formation, sources from a horizon no older than 96.4 Ma (Zanno et al., 2019; Tucker et al., 2020). The age ranges of *Moros intrepidus* and the Wayan tyrannosauroid, and their stratigraphic placement, indicate the Wayan form predates *Moros intrepidus* by ca. 1–5 Myr.



**Table 1.** Selected measurements of IMNH 2251/53975.

Measurement Description	Length (mm)
Proximodistal length of entire specimen	171
Proximodistal length of lesser trochanter	51
Proximodistal length of fourth trochanter	53
Maximum anteroposterior width of lesser trochanter	23
Mediolateral length of femoral head	41
Circumference of shaft immediately below fourth trochanter	92

Recognition and description of this specimen provide additional data points to the meager record of North American tyrannosauroids between the Albian and Turonian. In addition, the Wayan tyrannosauroid adds to the limited but growing knowledge of the faunal composition of the WVA. The most common vertebrate taxon within the WVA is the neornithischian *Oryctodromeus cubicularis* (Krumenacker, 2017, 2019; Krumenacker et al., 2019). The assemblage also comprises many other as yet poorly represented taxa (Dorr, 1985; Weishempal et al., 2002; Krumenacker, 2010, 2019; Krumenacker et al., 2016). Current data indicate some general similarities in faunal composition between the Wayan Formation and the Mussentuchit Member of the Cedar Mountain Formation (Krumenacker et al., 2019). The only species currently shared by those two faunas are the multituberculate mammals *Paracimexomys perplexus* Eaton and Cifelli, 2001, and *Bryceomys intermedius* Eaton and Cifelli, 2001 (Krumenacker et al., 2019; Weaver et al., 2019). The degree to which this disparity between geological units may represent paleogeographical and paleoenvironmental factors, sampling biases, and/or temporal differences is poorly constrained. Additional research is needed to provide better information concerning the faunal relationships of the Mussentuchit Member and the Wayan Formation. Although only general correlations are currently possible, the presence of a *Moros*-like tyrannosauroid in the geologically proximate Wayan Formation demonstrates another faunal similarity to the Mussentuchit Member of the Cedar Mountain Formation.

## Conclusions

The partial left femur IMNH 53975 is the first skeletal evidence for a tyrannosauroid from the Wayan Formation (late Albian–Cenomanian) of southeastern Idaho. This femur is similar in size and morphology to that of *Moros intrepidus* and the significantly younger *Suskityrannus hazelae*, but lacks the femoral autapomorphy diagnostic for *Moros intrepidus*. This difference indicates that the Wayan tyrannosauroid is a distinct form, which predates *Moros intrepidus* by a ca. 1–5 Myr.

Histological evidence indicates the Wayan form grew at rates similar to those of other early tyrannosauroids such as *Moros intrepidus*, in contrast to more rapidly growing later tyrannosauroids. The Wayan specimen came from an individual that died prior to attaining skeletal maturity and represents an immature animal, smaller than *Moros intrepidus*, with a minimum age of five years, whose adult size remains unknown.

This Wayan Vaughn Assemblage provides critical paleogeographic and chronostratigraphic data, being composed of taxa that represented lineages that were soon to diversify and dominate the

later Late Cretaceous. The Wayan tyrannosauroid provides another data point in the rise of tyrannosauroids and the development of the characteristic Late Cretaceous assemblages typified by tyrannosauroids, hadrosauroids, ankylosaurs, thescelosaurs, and ceratopsids. Continuing work in the Wayan Formation and correlative geological units holds promise for more data to document this critical time in vertebrate evolution.

## Acknowledgments

The specimen was collected under authorization through permit from Caribou Targhee National Forest. We thank D. Wheeler for assistance with the permitting process. S. Nesbitt provided useful information allowing comparisons to *Suskityrannus hazelae*. N. Campione, A. Dececchi, and R. Hickman assisted with mass estimation for the specimen. We thank A. Giterman for molding/casting and processing the osteohistological sections of IMNH 53975. The continued generosity of R. Simon provided funding that facilitated discovery of this specimen. The excellent teaching assistance of M. Blackburn that expedited the preparation of this manuscript is acknowledged. A. Morgan instructed LK in ways to expedite some figures, and A. Barker retrieved a relevant and useful printout for LK from the MVMS teachers' lounge. The expedient and beneficial comments and suggestions of both reviewers, which improved this manuscript, are acknowledged, and appreciated.

## References

- Brusatte, S.L., Averianov, A., Sues, H.-D., Muir, A. and Butler, I.B., 2016, New tyrannosauroid from the mid-Cretaceous of Uzbekistan clarifies evolution of giant body sizes and advanced senses in tyrant dinosaurs: Proceedings of the National Academy of Sciences of the United States of America, v. 113, p. 3447–3452.
- Campione, N.E., Evans, D.C., Brown, C.M., and Carrano, M.T., 2014, Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions: Methods in Ecology and Evolution, v. 5, p. 913–923.
- Carr, T.D., Williamson, T.E., Britt, B.B., and Stadtman, K., 2011, Evidence for high taxonomic and morphologic tyrannosauroid diversity in the Late Cretaceous (late Campanian) of the American Southwest and a new short-skulled tyrannosauroid from the Kaiparowits Formation of Utah: Naturwissenschaften, v. 98, p. 241–246.
- Castanet, J., Francillon-Viellet, H., Meunier, F.J., and Ricqlès, A. de, 1993, Bone and individual aging, in Hall, B.K., ed., Bone. Volume 7: Bone Growth. B: Boca Raton, Florida, CRC Press, p. 245–283.
- Dorr, J.A., Jr., 1985, Newfound early Cretaceous dinosaurs and other fossils in southeastern Idaho and westernmost Wyoming: University of Michigan, Contributions from the Museum of Paleontology, v. 27, p. 73–85.
- Eaton, G., and Cifelli, R. L., 2001, Multituberculate mammals from near the Early-Late Cretaceous boundary, Cedar Mountain Formation, Utah: Acta Palaeontologica Polonica, v. 46, p. 453–518.
- Eriksen, A.M.H., Nielsen, T.K., Matthiesen, H., Carøe, C., Hansen, L.H., Gregory, D.J., Turner-Walker, G., Collins, M.J., and Gilbert, M.T.P., 2020, Bone biodeterioration—the effect of marine and terrestrial depositional environments on early diagenesis and bone bacterial community: PLoS ONE, v. 15, e0240512. <https://doi.org/10.1371/journal.pone.0240512>.
- Funston, G.F., Tsogtbaatar, C., Tsogtbaatar, K., Kobayashi, Y., Sullivan, C., and Currie, P.J., 2020, A new two-fingered dinosaur sheds light on the radiation of Oviraptorosauria: Royal Society Open Science, v. 7, 201184. <https://doi.org/10.1098/rsos.201184>.
- Gauthier, J.A., 1986, Saurischian monophyly and the origin of birds, in Padian, K., ed., The Origin of Birds and the Evolution of Flight: Memoirs of the California Academy of Sciences, vol. 8, p. 1–55.
- Huene, F. von, 1914, Das natürliche System der Saurischia: Zentralblatt für Mineralogie, Geologie und Paläontologie B, v. 1914, p. 154–158.
- Kirkland, J.I., Burge, D., and Gaston, R., 1993, A large dromaeosaurid (Theropoda) from the Lower Cretaceous of eastern Utah: Hunteria, v. 2, n. 10, p. 1–16.

- Krumenacker, L.J., 2010, *Chronostratigraphy and paleontology of the mid-Cretaceous Wayan Formation of Idaho, with a description of the first Oryctodromeus specimens from Idaho [M.S. thesis]*: Provo, Utah, Brigham Young University.
- Krumenacker, L.J., 2017, *Osteology, phylogeny, taphonomy, and ontogenetic histology of Oryctodromeus cubicularis from the middle Cretaceous (Albian-Cenomanian) of Montana and Idaho [Ph.D. dissertation]*: Bozeman, Montana, Montana State University.
- Krumenacker, L.J., 2019, Paleontological and chronostratigraphic correlations of the mid-Cretaceous Wayan/Vaughn depositional system of southwestern Montana and southeastern Idaho: *Historical Biology*, v. 32, p. 1301–1311.
- Krumenacker, L.J., Varricchio, D.J., Wilson, G.P., and Robison, S., 2014, The Robison Bonebed: a preliminary report on the most diverse vertebrate fossil site known from the mid-Cretaceous Wayan Formation of Idaho: *Geological Society of America Program and Abstracts 2014*, p. 26. <https://gsa.confex.com/gsa/2014RM/webprogram/Paper238289.html>.
- Krumenacker, L.J., Simon, J.D., Scofield, G., and Varricchio, D.J., 2016, Theropod dinosaurs from the Albian–Cenomanian Wayan Formation of eastern Idaho: *Historical Biology*, v. 29, p. 170–186.
- Krumenacker, L.J., Varricchio, D.J., Wilson, J.P., Martin, A. and Ferguson, A., 2019, Taphonomy of and new burrows from *Oryctodromeus cubicularis*, a burrowing neornithischian dinosaur, from the mid-Cretaceous (Albian-Cenomanian) of Idaho and Montana, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 530, p. 300–311.
- Lamanna, M.C., Sues, H.-D., Schachner, E.R., and Lyson, T.R., 2014, A new large-bodied oviraptorosaurian theropod dinosaur from the latest Cretaceous of Western North America: *PLoS ONE*, v. 9, e92022. <https://doi.org/10.1371/journal.pone.0092022>.
- Lambe, L. M., 1914, On a new genus and species of carnivorous dinosaur from the Belly River Formation of Alberta, with a description of *Stephanosaurus marginatus* from the same horizon: *Ottawa Naturalist*, v. 28, p. 13–20.
- Lamm, E.T., 2013, Preparation and sectioning of specimens, in Padian, K., and Lamm, E.T., eds., *Bone Histology of Fossil Tetrapods: Advancing Methods, Analysis, and Interpretation*: Berkeley, University of California Press, p. 55–160.
- Li, D., Norell, M.A.; Gao, K., Smith, N.D. and Makovicky, P.J., 2009, A longirostrine tyrannosauroid from the Early Cretaceous of China: *Proceedings of the Royal Society B: Biological Sciences*, v. 277, p. 183–190.
- Lü, J., Yi, L., Zhong, H., Wei, X., 2013, A new Oviraptorosaur (Dinosauria: Oviraptorosauria) from the late Cretaceous of southern China and its paleoecological implications: *PLoS ONE*, v. 8, e80557. <https://doi.org/10.1371/journal.pone.0080557>.
- Makovicky, P., Kobayashi, Y., and Currie, P.J., 2004, Ornithomimosauria, in Weishampel, D.B., Dodson, P., and Osmólska, H., eds., *The Dinosauria*, 2<sup>nd</sup> ed.: Berkeley, University of California Press, p. 137–150.
- Marsh, O.C., 1881, Principal characters of American Jurassic dinosaurs. Part V: *American Journal of Science*, ser. 3, v. 21, p. 417–423.
- Nesbitt, S.J., Denton, R.K., Loewen, M.A., Brusatte, S.L., Smith, N.D., Turner, A.H., Kirkland J.I., McDonald, A.T., and Wolfe, D.G., 2019, A mid-Cretaceous tyrannosauroid and the origin of North American end-Cretaceous dinosaur assemblages: *Nature Ecology & Evolution*, v. 3, p. 892–899.
- Norell, M.A. and Makovicky, P.J., 1999, Important features of the dromaeosaurid skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*: *American Museum Novitates*, v. 3282, p. 1–44.
- Osborn, H.F., 1905, *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs: *Bulletin of the American Museum of Natural History*, v. 21, p. 259–265.
- Owen, R., 1842, Report on British fossil reptiles. Part II: Report of the Eleventh Meeting of British Association for Advancement of Science, Plymouth, p. 60–204.
- Padian, K., Lamm, E. T. and Werning, 2013, Selection of specimens, in Padian, K., and Lamm, E.T., eds., *Bone Histology of Fossil Tetrapods: Advancing Methods, Analysis, and Interpretation*: Berkeley, University of California Press, p. 35–54.
- Ross, J.B., Ludvigson, G.A., Möller, A., Gonzalez, L.A., and Walker, J.D. 2017, Stable isotope paleohydrology and chemostratigraphy of the Albian Wayan Formation from the wedge-top depozone, North American Western Interior Basin: *Science China Earth Science*, v. 60, p. 44–57.
- Rubey, W.W., 1973, New Cretaceous formations in the western Wyoming thrust belt: *U.S. Geological Survey Bulletin 1372-I*, p. 1–35.
- Schmitt, J.G., and Moran, M.E., 1982, Stratigraphy of the Cretaceous Wayan Formation, Caribou Mountains, southeastern Idaho thrust belt: *University of Wyoming Contributions to Geology*, v. 21, p. 55–71.
- Trueman, C.N., and Martill, D.M., 2002, The long-term survival of bone: the role of bioerosion. *Archaeometry*, v. 44, p. 371–382.
- Tucker, R.T., Zanno, L.E., Huang, H.-Q., and Makovicky, P.J., 2020, A refined temporal framework for newly discovered fossil assemblages of the upper Cedar Mountain Formation (Mussentuchit Member), Mussentuchit Wash, Central Utah: *Cretaceous Research*, v. 110, 104384. <https://doi.org/10.1016/j.cretres.2020.104384>.
- Turner, A.H., Makovicky, P.J., and Norell, M.A., 2012, A review of dromaeosaurid systematics and paravian phylogeny: *Bulletin of the American Museum of Natural History*, v. 371, p. 1–206.
- Turner-Walker, G., 2019, Light at the end of the tunnels? The origins of microbial bioerosion in mineralised collagen: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 529, p. 24–38.
- Varricchio, D.J., Martin, A.J., and Katsura, Y., 2007, First trace and body fossil evidence of a burrowing, denning dinosaur: *Proceedings of the Royal Society B*, v. 274, p. 1361–1368.
- Weaver, L.N., Wilson, G.P., Krumenacker, L. J., McLaughlin, K., Moore, J.R., and Varricchio, D.J., 2019, New multituberculate mammals from the mid-Cretaceous (lower Cenomanian) Wayan Formation of southeastern Idaho and implications for the early evolution of Cimolodonta: *Journal of Vertebrate Paleontology*, v. 39, e1604532. <https://doi.org/10.1080/02724634.2019.1604532>.
- Weishampel, D.B., Akersten, W.A., McCrady, A.D., and Meers, M.B., 2002, New Early Cretaceous dinosaur remains, including possible ceratopsians, from the Wayan Formation of eastern Idaho, in Akersten, W.A., McDonald, H.G., Meldrum, D.J., and Thompson, M.E., eds., *And Whereas... Papers on the Vertebrate Paleontology of Idaho Honoring John A. White*: Idaho Museum of Natural History Occasional Paper, v. 37, n. 2, p. 5–17.
- Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q., and Jia, C., 2004, Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids: *Nature*, v. 431, p. 680–684.
- Xu, X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.A., Eberth D.A., Jia, C., and Zhao, Q., 2006, A basal tyrannosauroid dinosaur from the Late Jurassic of China: *Nature*, v. 439, p. 715–718.
- Yu, Y., Wang, K., Chen, S., Sullivan, C., Wang, S., Wang, P., and Xu, X., 2018, A new caenagnathid dinosaur from the Upper Cretaceous Wangshi Group of Shandong, China, with comments on size variation among oviraptorosaurs: *Scientific Reports*, v. 8, 5030. <https://doi.org/10.1038/s41598-018-23252-2>.
- Zanno, L.E., and Makovicky, P.J., 2011, On the earliest record of Cretaceous tyrannosauroids in western North America: implications for an Early Cretaceous Laurasian interchange event: *Historical Biology*, v. 23, p. 317–325.
- Zanno, L.E., and Makovicky, P.J., 2013, Neovenatorid theropods are apex predators in the Late Cretaceous of North America: *Nature Communications*, v. 4, 2827. <https://doi.org/10.1038/ncomms3827>.
- Zanno, L.E., Tucker, R.T., Canoville, A., Avrahami, H.M., Gates, T.A., and Makovicky, P.J., 2019, Diminutive fleet-footed tyrannosauroid narrows the 70-million year gap in the North American fossil record: *Biology Communications*, v. 2, 64. <https://doi.org/10.1038/s42003-019-0308-7>.
- Zelenitsky, D.K., Carpenter, K., and Currie, P.J., 2000, First record of elongatoolithid theropod eggshell from North America: the Asian oogenus *Macroelongatoolithus* from the Lower Cretaceous of Utah: *Journal of Vertebrate Paleontology*, v. 20, p. 130–138.

Accepted: 2 May 2022