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ARTICLE

FIRST OCCURRENCE OF A TYRANNOSAUROID DINOSAUR FROM THE LOWER CAMPANIAN MERCHANTVILLE FORMATION OF DELAWARE, USA

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ABSTRACT

This study provides a detailed osteological description of an isolated proximal caudal centrum and two nearly complete isolated metatarsals II and IV of the left foot of a gracile theropod dinosaur from the Lower Campanian of the Merchantville Formation in northern Delaware, USA. The caudal centrum and the metatarsals are referred to Tyrannosauroidea. The centrum is not well preserved, and thus not diagnostic; however, both metatarsals are diagnostic. The referral to Tyrannosauroidea is supported by several morphological features, including extensive surfaces on metatarsals II and IV for the articulation with metatarsal III, and a characteristic low, slightly convex muscle scar on metatarsal IV developed as a thin low ridge located on the posterior surface between the M. gastrocnemius pars lateralis insertion scar and the metatarsal III articular surface. This ridge has been previously interpreted as the plantar ridge, which is present in some derived Late Campanian tyrannosauroid taxa. Additionally, metatarsal IV has a deep medial notch for the accommodation of an "L"– shaped proximal articulation of metatarsal III, and a "U"– shaped proximal articular end. The Merchantville Formation tyrannosauroid exhibits arctometatarsalian metatarsals, as do tyrannosaurids. The Merchantville Formation tyrannosauroid is differentiated from other known basal and derived tyrannosaurids by having a characteristically shaped proximal articular surface of metatarsal II in which the proximal and posterior ends lie on the long axis of the proximal articular surface. However, the posterior proximal articular surface of metatarsal II is not as strongly angled laterally as in more derived tyrannosauroids. The Merchantville Formation tyrannosauroid adds to the record of Appalachian tyrannosauroid, evolution and paleostratigraphic position, and provides new morphological information about the metatarsal anatomy of these iconic theropods.

Key words : Tyrannosauroidea, Theropoda, Upper Cretaceous, early Campanian, Delaware, United States

INTRODUCTION

The skeletal fossil remains of eastern North American (Appalachian) tyrannosauroid dinosaurs are rare (Schwimmer et al., 1993; Schwimmer, 1989, 2004; Carr et al., 2005). They are found in the Cenomanian–Turonian and Campanian–Maastrichtian deposits throughout this part of the continent, suggesting a long stratigraphic range and wide paleobiogeographic distribution of these iconic theropods (e.g., Schwimmer, 1989, 2004; Schwimmer et al., 1993; Carr et al., 2005; Brusatte et al., 2011; Dalman et al., 2016). In contrast, the Upper Cretaceous terrestrial deposits of Laramidia preserve one of the richest, most diverse assemblages of tyrannosauroid fossils found anywhere in the world, being distributed from modern day Alaska to modern day Mexico (e.g., Russell, 1970; Carr and Williamson, 2010; Carr et al., 2011; Lehman and Wick, 2012; Loewen et al., 2013; Fiorillo and Tykoski, 2014; Peecook et al., 2014; Dalman and Lucas, 2015, 2016; Serrano-Brañas et al., 2017). The Laramidian tyrannosauroids comprise both basal and derived forms, with the derived forms divisible into two subfamilies: Albertosaurinae and Tyrannosaurinae (Currie, 2003, 2005). The Appalachian tyrannosauroids, on the other hand, comprise basal forms, and most fall outside of these clades (e.g., Carr et al., 2005; Brusatte et al., 2011; Brusatte and Carr, 2016).

The best known and most complete Appalachian tyrannosauroid taxa are *Appalachiosaurus montgomeriensis* (Carr et al., 2005) and *Dryptosaurus aquilunguis* (Marsh, 1877). *Appalachiosaurus* is the more completely known taxon, and is from the Middle Campanian of Alabama, USA, whereas *Dryptosaurus* is based on several isolated cranial and postcranial skeletal elements from

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the Upper Maastrichtian of New Jersey, USA. The osteological descriptions by Carpenter et al. (1997) and the phylogenetic analyses by Carr et al. (2005), Brusatte et al. (2010, 2011), and, most recently, by Brusatte and Carr (2016), place these taxa within the Tyrannosauroidea. However, in the paleobiogeographic analysis of Brusatte and Carr (2016), *Dryptosaurus* has been recovered as a more derived tyrannosauroid. Although fragmentary, the Appalachian tyrannosauroids provide important information about the evolution, taxonomic diversity, and paleogeographic distribution of these theropods throughout North America during most of the Cretaceous.

The discovery in 1975 by Ralph Johnson and Ray Meyer (Monmouth Amateur Paleontologists Society in Long Branch, New Jersey) of an isolated proximal caudal centrum and two nearly complete left metatarsals II and IV in the lower Campanian Merchantville Formation (Upper Cretaceous) along the Chesapeake and Delaware Canal in northern Delaware has remained the subject of unresolved taxonomic relationships. Previously, Horner (1979) referred the specimens to Ornithomimidae indeterminate without a formal description. However, based on their overall morphology, the specimens are here referred to Tyrannosauroidea, and thus represent one of the oldest occurrences of Appalachian tyrannosauroids. These specimens predate *Appalachiosaurus* and *Dryptosaurus* and some of the Laramidian tyrannosauroids such as *Albertosaurus*, *Daspletosaurus*, *Gorgosaurus*, *Lythronax*, *Nanotyrannus*, *Nanuqsaurus*, and *Tyrannosaurus*. The identification of tyrannosauroids in a stratigraphically older unit provides further support for a relatively wide paleobiogeographic distribution of these theropods during the Late Cretaceous in North America.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, New York, USA; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **IGM**, Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, México; **MIWG**, Museum of Isle of Wight Geology, Isle of Wight, England, UK; **NMC**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; **PIN**, Palaeontological Institute, Moscow, Russia; **RMM**, Red Mountain Museum, Birmingham, Alabama, USA; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **TMM**, Texas Memorial Museum, Austin, Texas, USA; **UMNH**, Natural History Museum of Utah, Salt Lake City, Utah, USA; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut (formerly at PU, Division of Vertebrate Paleontology Princeton University, Princeton, New Jersey), USA; **ZPAL**, Institute of Palaeobiology of the Polish Academy of Sciences, Warsaw, Poland.

Geologic Setting

The isolated caudal centrum and two metatarsals described here were found at the locality along the north bank of the Chesapeake and Delaware Canal, ~ 1.2 km east of Summit Bridge Route 301 and 0.8 km north of Summit Delaware (Fig. 1). In the bank of the Chesapeake and Delaware Canal the following section is exposed, in ascending order (Owens et al., 1970): (1) Merchantville Formation; (2) Englishtown Formation; (3) Marshalltown Formation; and (4) Mount Laurel Formation. These geologic formations originated from sediments eroded from the Appalachian Mountains to the west.

The Merchantville Formation is located in northern Delaware and represents a mixture of terrestrial and lagoonal environments (Baird and Galton, 1981). The sediments of the formation are light to dark-gray, very micaceous, glauconitic, very silty, fine to very fine-grained sand and silt, and were deposited during the Early Campanian, ~ 83.5 Ma (Petters, 1976; Ramsey, 2005). The thickness of the formation is usually ~ 7 m, but ranges up to ~ 36 m in some places (Owens et al., 1970; Lauginiger, 1988; Ramsey, 2005).

The base of the Merchantville Formation is glauconitic sand that is covered by the silt of the main part of Merchantville Formation, which in turn, grades into the quartz sands of the

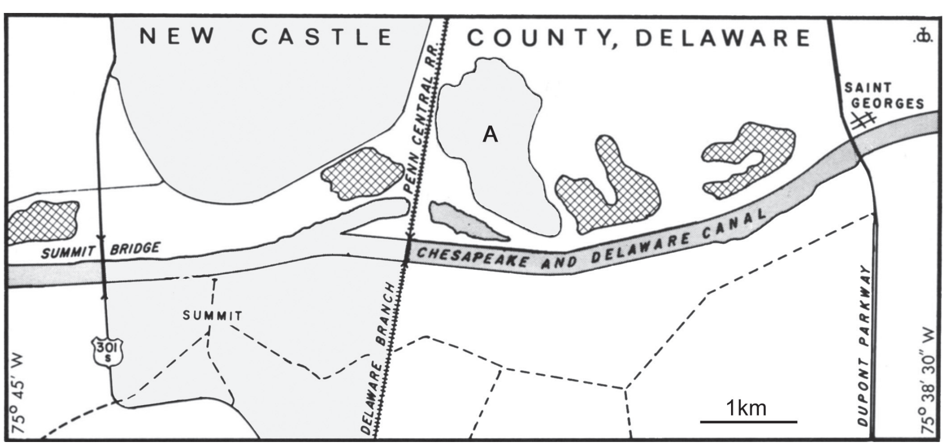

FIGURE 1. Map of the north bank of the Chesapeake and Delaware Canal, Delaware. **A,** Locality of the Merchantville Formation tyrannosauroid , ~ 1.2 km east of Summit Bridge, Route 301 and 0.8 km north of Summit Delaware (modified from Baird and Galton, 1981).

Englishtown Formation (Curran, 1985). The sands that contain glauconite were deposited in deep water, whereas the quartz silts and sands indicate shallow water. Curran (1985) interpreted the Englishtown Formation as deposits in the upper shore face lower foreshore zone. Exposures of the Englishtown Formation are marked by an unconformity that separates it from the overlying Marshalltown Formation.

The Merchantville Formation yields a fragmentary but significant Upper Cretaceous vertebrate fauna composed of chondrichthyans, osteichthyans, crocodylians, dinosaurs, marine reptiles such as mosasaurs, pterosaurs, and turtles (e.g., Baird and Galton, 1981; Lauginiger, 1988; Gallagher, 1993, 2005). The dinosaurian fauna includes hadrosaurids and medium-sized, non-avian theropods (e.g., Baird and Horner, 1977; Horner, 1979; Lauginiger, 1988; Gallagher, 2004; Weishampel et al., 2004; Weishampel, 2004, 2006).

SYSTEMATICS

YPM VPPU 021795, metatarsals II and IV of the left pes, and YPM VPPU 022416 caudal centrum, were originally considered as belonging to the Ornithomimidae (Horner, 1979). However, in this study they are reassigned to Tyrannosauroidea based on several key characters, including the "D"– shaped proximal articular surface of metatarsal II, the lateral notch for the articulation with the proximal end of metatarsal III, large articular surfaces on the shaft for the articulation with metatarsal III, the "U"– shaped proximal articular surface of metatarsal IV and the medial notch for the articulation with the "L"– shaped proximal end of metatarsal III.

DINOSAURIA Owen, 1842
THEROPODA Marsh, 1881
COELUROSAURIA von Huene, 1914
TYRANNOSAUROIDEA Walker, 1964

Tyrannosauroidea indeterminate

Material.—YPM VPPU 021795, metatarsal II and IV of the left pes, YPM VPPU 022416, caudal centrum.

Locality, horizon and age .—North bank of the Chesapeake and Delaware Canal, Delaware, ~ 1.2 km east of Summit Bridge, Route 301 and 0.8 km north of Summit Delaware. Merchantville Formation, Late Cretaceous (Early Campanian) (Fig. 1).

DESCRIPTION

Vertebra.—YPM VPPU 022416 is identified as an anterior caudal centrum (Fig. 2). The centrum is not well-preserved and lacks important diagnostic features. It is crushed and heavily eroded on one side, whereas the other side preserves the shape and part of the original outer bone surface. The centrum is not diagnostic due to its poor preservation; however, the overall shape is consistent with that of a tyrannosauroid caudal centrum. The centrum was found with the metatarsals described below, suggesting that the centrum and both metatarsals may belong to the same animal.

Metatarsals.—The left metatarsal II, YPM VPPU 021795, is missing only the distal condyle (Fig. 3). The length of the preserved metatarsal is 30 cm (Table 1).

As in other tyrannosauroids (e.g., Brochu, 2003; Carr et al., 2005), the proximal end of the metatarsal II, YPM VPPU 021795 is "D"– shaped. The proximal articular surface is larger than that of the metatarsal IV and is expanded mediolaterally and anteroposteriorly beyond the metatarsal shaft. The articular surface in proximal view is more expanded mediolaterally in the anterior region (5 cm) than in the posterior region (3.5 cm). The anteroposterior length of the proximal articular surface of the metatarsal II is 8 cm. The surface ventral to the proximal articulation has a "swollen" appearance, except for the lateral surface, which is flat. The lateral surface of the proximal end has a characteristic shallow and narrow lateral notch for articulation with the proximal end of metatarsal III. The length of the notch is 3 cm, and the width 1.5 cm. Anterior to this notch is a flat articular surface, which is partially reconstructed, that is 4 cm long and 3 cm wide. This surface contacted the proximal anteromedial surface of metatarsal IV, as in other tyrannosauroids (e.g., Brochu, 2003). Directly posterior to the lateral notch is a flat articular surface for metatarsal III that is 3 cm long and 3 cm wide anteroposteriorly. Distal to this surface is an elongate rugose surface that is oriented anterolaterally. This rugosity marks the insertion site for M. tibialis anterior (Carrano and Hutchinson, 2002). Distal to the insertion site for M. gastrocnemius pars lateralis is a larger articular surface with smooth and subtle texture that occupies half the length of the lateral shaft of metatarsal II. This characteristic surface is referred to as the articular scar for metatarsal III and is present in all known tyrannosauroids (e.g. Brochu 2003). Both articular surfaces are separated from each other by a characteristic elongate ridge. The far larger articular surface originates at the distal end of this ridge and extends farther distally. The larger surface is narrow (approximately 3 cm), and at the proximal extremity it begins to flare anteroposteriorly towards the distal end of the shaft.

The shaft of metatarsal II is relatively straight in anterior and posterior aspect, whereas in lateral and medial aspect the shaft is slightly convex in a way that is characteristic of all known tyrannosauroids (e.g., Carrano and Hutchinson, 2002; Brochu, 2003; Carr et al., 2005; Brusatte et al., 2010). The posterior surface of the shaft is flat, and the anterior surface is strongly convex. The medial and lateral corners of the posterior surface of the shaft are slightly convex. Anteroposteriorly, the shaft is broad and closely resembles the condition of derived tyrannosaurids. The posterior surface of the shaft has a posteromedially oriented, rugose, teardrop-shaped concavity, which is interpreted as the insertion site for M. gastrocnemius pars lateralis (e.g., Carrano and Hutchinson, 2002). Its position and overall morphology closely resemble those of known tyrannosaurids (e.g., Carrano and Hutchinson, 2002; Brochu, 2003; Carr et al., 2005).

The posteromedial surface of the metatarsal shaft contains two small rugosities (Fig. 4). The proximalmost rugosity is small.

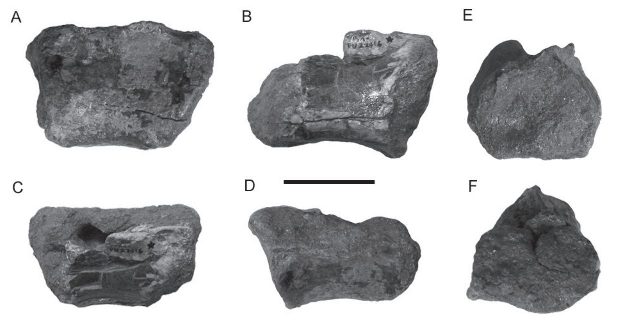

FIGURE 2. Tyrannosauroid proximal caudal vertebra (YPM VPPU 022416). **A,** right lateral view; **B,** left lateral view; **C,** dorsal view; **D,** ventral view; **E,** anterior view; **F,** posterior view. Bar = 5 cm.

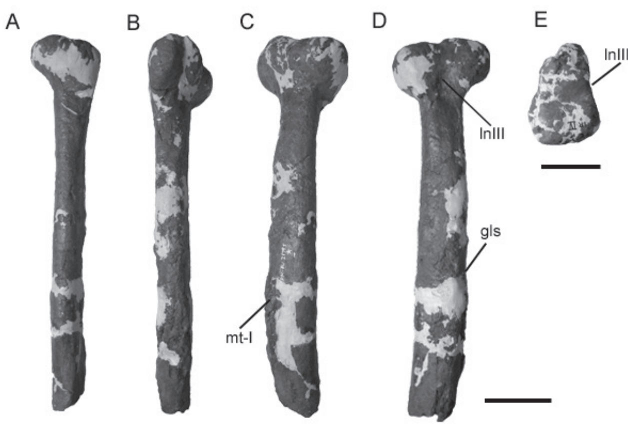

FIGURE 3. Tyrannosauroid left metatarsal II (YPM VPPU 021795). **A,** anterior view; **B,** posterior view; **C,** medial view; **D,** lateral view; **E,** proximal view. Abbreviations are in Appendix 1. Bar = 5 cm.

Directly distal to it is a much larger, teardrop-shaped rugosity that marks the surface attachment for metatarsal I (Brochu, 2003; Carrano et al., 2005; Hattori, 2016). However, there are competing interpretations of the scar on metatarsal II for the attachment of metatarsal I (e.g., Tarsitano and Hecht, 1980; Carrano and Hutchinson, 2002).

The left metatarsal IV, YPM VPPU 021795, is essentially complete (Fig. 5; Table 2). The total length of the preserved metatarsal is 38 cm, and its circumference is 9.5 cm at midshaft. The minimum circumference is 9.1 cm and is present in two regions of the shaft: distal to the proximal end and dorsal to the distal condyles. The metatarsal shaft is straight in all aspects. The distal portion of the shaft approximately 7.5 cm dorsal to the distal condyles is broken. When associated, the distal end is angled slightly laterally, and the lateral condyle is shorter than the medial condyle. The medial surface of the metatarsal shaft is flat, which indicates that metatarsal IV was tightly appressed to metatarsal III for its entire length.

The proximal articular surface of metatarsal IV YPM VPPU 021795 is "U"– shaped, and, in the posterior region, has a well-marked articulation for distal tarsal four (dt4) (e.g., Carrano and Hutchinson, 2002; Brochu, 2003; Brusatte et al., 2011; Lehman and Wick, 2012; Thomson et al., 2013; Peecook et al., 2014). The convex surface of the "U"– shaped proximal articular end faces laterally. A small semicircular rugosity located at the posterolateral edge of the proximal articulation marks the contact with metatarsal V (e.g., Carrano and Hutchinson, 2002). The medial surface of the proximal end of metatarsal IV has a characteristic narrow, but deep (2 cm) concave notch, against which the "L" – shaped proximal end of metatarsal III articulates (e.g., Holtz, 1994; Brochu, 2003; Lehman and Wick, 2012; Thomson et al., 2013; Peecook et al., 2014). The notch continues distally on the medial surface of the metatarsal IV for approximately 5 cm, but as it approaches the shaft it slightly widens and gradually tapers

TABLE 1. Measurements of the metatarsal II (YPM VPPU 021795). Measurements in mm. *(estimated length) refers to the length of the complete metatarsal.

Length	300.0 (estimated length 400)*
Proximal surface, circumference	211
Proximal surface, anteroposterior width	80.2
Proximal surface, mediolateral width	45.0
Midshaft, circumference	111
Midshaft, anteroposterior width	27.2
Midshaft, mediolateral width	28.2
Robusticity indices (RI)	0.3700 (with estimated length 0.2775)

TABLE 2. Measurements of metatarsal IV (YPM VPPU 021795). Measurements in mm *(estimated length) refers to the length of the complete metatarsal.

Length	310.5 (estimated length 350)*
Proximal surface, circumference	200
Proximal surface, anteroposterior width	55.0
Proximal surface, mediolateral width	50.0
Midshaft, circumference	98
Midshaft, anteroposterior width	22.0
Midshaft, mediolateral width	26.0
Robusticity indices (RI)	0.3156 (with estimated length 0.2800)

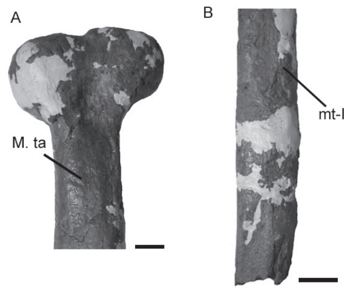

FIGURE 4. Tyrannosauroid posterolateral surface of the shaft of the left metatarsal II (YPM VPPU 021795) showing two small rugosities (M. ta and mt-1). Abbreviations are in Appendix 1. Bars = 2 cm.

as it merges into the medial surface of the shaft. Posterior to the medial notch is a "tear-drop"– shaped articular surface for metatarsal II, and anterior to the notch is the articular surface for metatarsal III (e.g., Brochu, 2003). Between the proximal notch for metatarsal III and the tear-drop articular facet lies an ovoid rugosity that is nearly twice as long as it is wide. This rugosity marks the insertion site for the M. tibialis anterior (e.g., Carrano and Hutchinson, 2002).

The posterior surface of the shaft is flat, and the anterior surface is convex. Together they give the proximal half of the shaft a subtriangular cross-section, with the sharpest corners situated medially and laterally. At mid-length, the shaft begins to curve and twists slightly laterally, and the curvature is visible at the broken distal end.

The posterior surface of the shaft of metatarsal IV has a distinct elongate rugosity, visible in lateral and medial aspects. The rugosity originates slightly distal to the proximal articular surface and extends for most of the shaft's length, although in the middle of the bone the rugosity curves gently laterally, and continues down the shaft in this trajectory. This elongated rugosity is interpreted as the insertion site for the M. gastrocnemius pars lateralis (e.g., Carrano and Hutchinson, 2002).

Located on the medial surface of the metatarsal shaft just ventral to the medial notch is an elongated, "tear-drop"– shaped surface, interpreted as the insertion site for the M. tibialis anterior (e.g., Carrano and Hutchinson, 2002). Approximately 6 cm distal to the proximal articular surface is another much larger articular surface for metatarsal III. It originates on the posteromedial surface of the metatarsal shaft and continues distally (e.g., Brochu, 2003; Peecook et al., 2014). However, near the midshaft

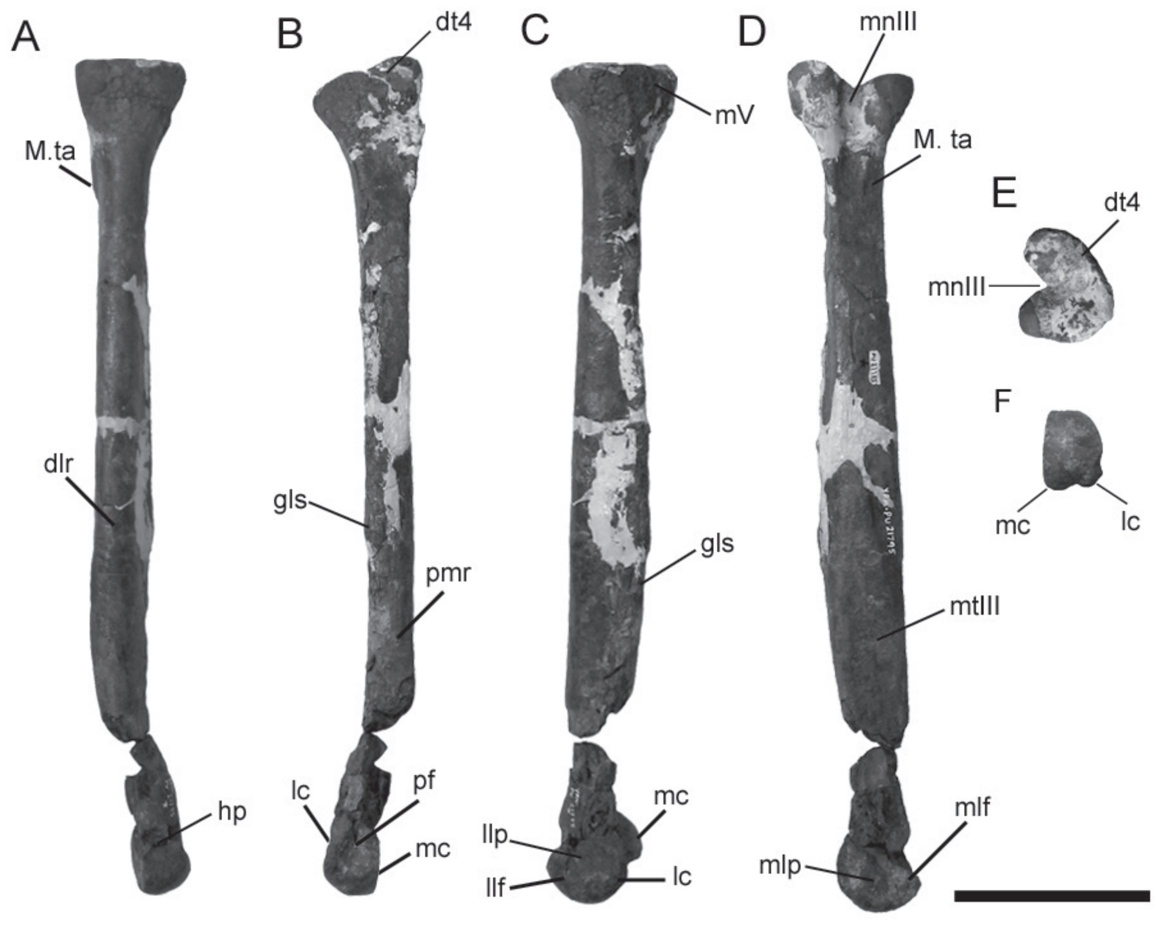

FIGURE 5. Tyrannosauroid left metatarsal IV (YPM VPPU 021795). **A,** anterior view; **B,** posterior view; **C,** lateral view; **D,** medial view; **E,** proximal; **F,** distal view. Abbreviations are in Appendix 1. Bar = 10 cm.

it begins to flare anteroposteriorly and extends near the distal end of the bone in such a way that it occupies the entire width of the shaft.

A characteristic low, distolaterally-trending ridge is situated on the anterior surface of the shaft. The ridge originates anteroventral to the insertion site for the M. tibialis anterior and extends distally nearly half the length of the shaft. At its terminal end the ridge gradually merges into the shaft, and the surface distal to it is flat and smooth. The posterior surface between the M. gastrocnemius pars lateralis insertion scar and the metatarsal III articular surface is slightly convex, with a muscle scar developed as a thin, low ridge, which has been interpreted as the plantar ridge by Thomson et al. (2013). The plantar ridge emerges from the articular surface for metatarsal III, and is oriented distolaterally. It extends along the posteromedial margin and continues distally for approximately 10 cm along the long axis of the distal portion of the shaft. It then merges with the dorsal surface of the lateral distal condyle.

The distal articular surface of the metatarsal IV is asymmetrical. The medial condyle is mediolaterally wider and anteroposteriorly longer than the lateral condyle. The lateral ligament pit is shallow, whereas the medial ligament pit is deep. In contrast, the lateral ligament fossa that surrounds the ligament pit is larger than the medial ligament fossa. Both fossae are not deeply inserted around the ligament pits. The anterior hyperextensor pit is a larger "U" – shaped depression situated proximal to the distal condyle. In posterior view, the condyles are separated by a deep intercondylar sulcus.

DISCUSSION

Horner (1979) previously referred the metatarsals II and IV (YPM VPPU 021795) to Ornithomimidae indeterminate. However, the metatarsals exhibit typical tyrannosauroid morphology. The suite of morphological characters that support the referral of YPM VPPU 021795 to a tyrannosauroid dinosaur include the "D"– shaped proximal articular surface of metatarsal II, the lateral notch for the articulation with the proximal end of metatarsal III, large articular surfaces on the shaft for the articulation with metatarsal III, the "U"– shaped proximal articular surface of metatarsal IV and the medial notch for the articulation with the "L"– shaped proximal end of the metatarsal III. On the basis of these characters, the proximal end of metatarsal III of YPM VPPU 021795 was pinched between metatarsals II and IV in a way characteristic of arctometatarsalian theropods (e.g., Holtz, 1994).

However, at the time when Horner referred the metatarsals to an indeterminate ornithomimid theropod, the fossil record of North American tyrannosauroids was less complete than it is today, and the term Arctometatarsalia (Holtz, 1994) had not yet been proposed. Theropods with arctometatarsalian feet include most of the tyrannosauroids, but also include other coelurosaurian families such as Alvarezsauridae, Avimimidae, Caenagnathidae, Ornithomimidae, Oviraptoridae, and Troodontidae, which all exhibit a pinched proximal end of metatarsal III between metatarsals II and IV. As noted in the description, the posterior surface of metatarsal IV of the Merchantville tyrannosauroid is slightly convex and has a muscle scar developed as a thin, low ridge situated between the M. gastrocnemius pars lateralis insertion scar and the metatarsal III articular surface.

Although the metatarsals of the Merchantville Formation tyrannosauroid exhibit the morphology of a derived tyrannosauroid, they can be differentiated from other known tyrannosauroids by the relatively straight proximal articular surface of metatarsal II. In general, the medial margin of the proximal articular surface of metatarsal II in more derived tyrannosauroids (e.g., *Appalachiosaurus*, *Bistahieversor*, *Gorgosaurus*, *Tarbosaurus*, and *Tyrannosaurus*) (Fig. 6) is strongly convex, and the posterior portion of the proximal end is angled laterally. As a result, the lateral notch in derived tyrannosauroids such as *Appalachiosaurus*, *Bistahieversor*, *Gorgosaurus*, and *Tyrannosaurus* is more pronounced than it is in the Merchantville Formation tyrannosauroid. The characteristic morphology of the proximal articular surface of metatarsal II (YPM VPPU 021795) most likely represents a basal condition shared with the Late Jurassic coelurid theropods that exhibit similar morphologies, such as *Coelurus fragilis*, *Ornitholestes hermanni* and *Tanycolagreus topwilsoni* (=*Stokesosaurus clevelandi*) (see Carpenter et al., 2005a; fig. 2.15, p. 44; Carpenter et al., 2005b; fig. 3.13, p. 68), and some Late Cretaceous ornithomimids such as *Gallimimus bullatus* (Osmólska et al., 1972) and *Ornithomimus velox* (Osborn, 1916) (Fig. 7). However, in *Gallimimus* (ZPAL Mg D-I /94) the posterior end of the proximal articular surface is more angled laterally than in the Merchantville tyrannosauroid or in *O. velox* (YPM VP 0542).

In the past decade and in recent years, detailed osteological and comparative anatomical studies of the lower appendicular skeletal

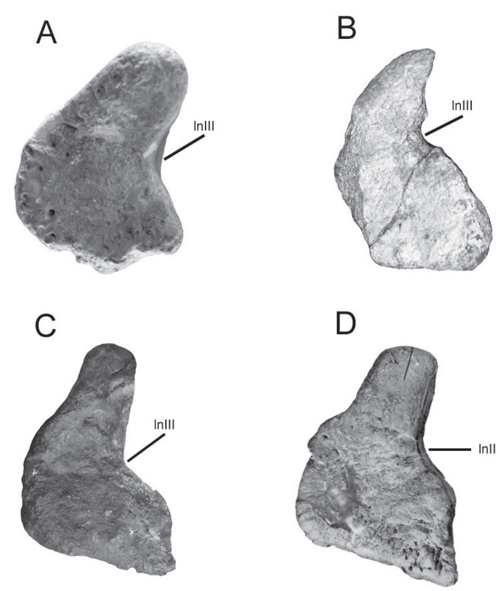

FIGURE 6. Tyrannosauroids left metatarsal II proximal view. **A,** *Appalachiosaurus montgomeriensis* (RMM 6670); **B,** *Bistahieversor sealeyi* (NMMNH P-25049); **C,** *Gorgosaurus libratus* (YPM VP 055672); **D,** *Tyrannosaurus rex* (FMNH PR2081). Not to scale.

elements of tyrannosauroid materials, particularly of new taxa, have been written (e.g., Carrano and Hutchinson, 2002; Snively and Russell, 2002; Brochu, 2003; Snively et al., 2004; Brusatte et al., 2012; Lehman and Wick, 2012; Thomson et al., 2013; Peecook et al., 2014; Hattori, 2016). These studies provide new information about the anatomy of tyrannosauroid metatarsals, which, among other known theropod families and other arctometatarsalians, are unique. The most notable morphological feature is the "L"– shaped proximal articular end of metatarsal III, which is present in both basal and derived tyrannosauroids. In other arctometatarsalian theropods (e.g., ornithomimosaurs) the lateral and medial surfaces of the proximal end of metatarsal III are flat and lack the "L"– shape morphology (Fig. 7).

At present it is not clear when and where the arctometatarsalian tyrannosauroids first evolved. However, based on fragmentary tyrannosauroid material from the Cenomanian of New Jersey, the arctometatarsalian tyrannosauroids were already present in Appalachia during an early stage of the Late Cretaceous. The recovery of fragmentary specimens and several diagnostic teeth pertaining to tyrannosauroids from the pre- and early Campanian deposits of Laramidia (e.g., Kirkland et al., 1997; Cifelli et al., 1997, 1999; Eaton et al., 1999; Parrish, 1999; Garrison et al., 2007; Larson, 2008; Zanno and Makovicky, 2011; Wick et al., 2015; Dalman and Lucas, 2016; Krumenacker et al., 2016) suggests that these theropods were already present in North America and had a wide paleobiogeographic and stratigraphic occurrence. The earliest recorded occurrence of tyrannosauroids in North America is from the Aptian/Albian deposits of the Cloverly Formation in Wyoming (Zanno and Makovicky, 2011) and the Wayan Formation of Idaho (Krumenacker et al., 2016).

For most of the Aptian/Albian, the eastern and western parts of North America were not separated by the inland seaway (Blakey, 2014), which allowed the dinosaurs, and, in particular the tyrannosauroids, to spread across the continent and inhabit various paleobiogeographic/ paleoecological niches. By the middle Coniacian (96 Ma), the inland seaway opened and remained open for approximately 25 million years (Blakey, 2014). The seaway started to close in the south during the late Campanian/ early Maastrichtian, forming a land bridge where Colorado and New Mexico are today (Blakey, 2014). According to these data, during these 25 million years of separation the Appalachian and Laramidian tyrannosauroids evolved in isolation. The most parsimonious interpretation is that the Appalachia tyrannosauroids are the descendants of ancestors that came from Laramidia during the middle Cenomanian or perhaps during the Aptian.

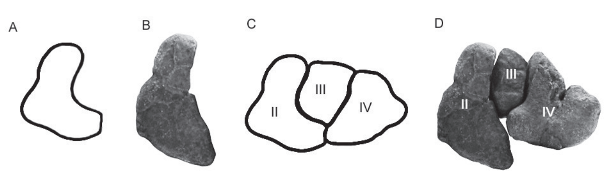

FIGURE 7. Proximal articular surface of the left metatarsal II. **A,** *Gallimimus bullatus* (interpretive drawing); **B,** *Ornithomimus velox* (YPM VP 0542). Interpretive drawing of associated metatarsals II, III and IV. **C,** *Gallimimus bullatus*; **D,** *Ornithomimus velox* (YPM VP 0542). Not to scale.

For the most part, the vertebrate faunas, particularly the dinosaurian faunas, are poorly known and understood from the Cretaceous of eastern North America (Appalachia). The Merchantville fauna is thought to represent a mixture of terrestrial and lagoonal environments (Baird and Galton, 1981; Robb, 2004). Regardless, it seems apparent that these animals would have been living near the shoreline of the western Atlantic Ocean in eastern Appalachia. Indeed, many of the vertebrates known from the Merchantville Formation convey a lagoonal or marine environment, including the chondrichthyans, osteichthyans, and mosasaurs. Pterosaurs, as volant animals, could easily be found in many environments, although marine and nearshore environments tend to be better localities to preserve their remains. The skeletal remains of turtles and crocodylians are expected in such an environment. While the dinosaurian fauna is minimal and rare, the presence of the Merchantville tyrannosauroid with hadrosaurids adds new information to the paleoecology of eastern Appalachia during the early Campanian. Hadrosaurids and tyrannosauroids were widespread throughout North America during the Late Cretaceous. The rarity of dinosaur specimens from these units in eastern North America makes each potentially more important and useful for understanding the evolution and paleobiogeography of these animals.

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REFERENCES

Baird, D., and P. Galton. 1981. Pterosaur bones from the Upper Cretaceous of Delaware. Journal of Vertebrate Paleontology 1: 67–71.

Baird, D., and J. R. Horner. 1977. A fresh look at the dinosaurs of New Jersey and Delaware. New Jersey Academy of Science Bulletin 22: 50A.

Blakey, R. C. 2014. Paleogeography and paleotectonics of the Western Interior Seaway, Jurassic-Cretaceous of North America. Tulsa Geological Society Luncheon Meeting 1–72 pp. (www.searchanddiscovery.com/documents /2014/ 30392blakey/idex_blakey.pdf)

Brochu, C. A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. Journal of Vertebrate Paleontology Memoir 22: 1–138.

Brusatte, S. L., R. B. J. Benson and M. A. Norell. 2011. The anatomy of *Dryptosaurus aquilunguis* (Dinosauria: Theropoda) and a review of its tyrannosauroid affinities. American Museum Novitates 3717: 1–53.

Brusatte, S. L., and T. D. Carr. 2016. The phylogeny and evolutionary history of tyrannosauroid dinosaurs. Scientific Reports, 6:20252/DOI:10.10138/srep20252.

Brusatte, S. L., T. D. Carr and M. A. Norell. 2012. The osteology of *Alioramus*, a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. Bulletin of the American Museum of Natural History 366: 1– 197.

Brusatte, S. L., M. A. Norell, T. D. Carr, G. M. Erickson, J. R. Hutchinson, A. M. Balanoff, G. S. Bever, J. N. Choiniere, P. J. Makovicky and X. Xu. 2010. Tyrannosaur paleobiology: new research on ancient exemplar organisms. Science 329: 1481–1485.

Carpenter, K., M. Clifford and K. Cloward. 2005a. New small theropod from the Upper Jurassic Morrison Formation of Wyoming; pp. 23–48 *in* Carpenter, K., (ed.), The Carnivorous Dinosaurs. Indiana University Press, Bloomington and Indianapolis, Indiana.

Carpenter, K., C. Miles, J. H. Ostrom and K. Cloward. 2005b. Redescription of the small maniraptoran theropods *Ornitholestes* and Coelurus from the Upper Jurassic Morrison Formation of Wyoming; pp. 49–71 *in* Carpenter, K., (ed.), The Carnivorous Dinosaurs. Indiana University Press, Bloomington and Indianapolis, Indiana.

Carpenter, K., D. Russell, D. Baird and R. Denton. 1997. Redescription of the holotype of *Dryptosaurus aquilunguis* (Dinosauria: Theropoda) from the Upper Cretaceous of New Jersey. Journal of Vertebrate Paleontology 17: 561–573.

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

Carr, T. D., T. E. Williamson and D. R. Schwimmer. 2005. A new genus and species of tyrannosauroid from the Late Cretaceous (Middle Campanian) Demopolis Formation of Alabama. Journal of Vertebrate Paleontology 25: 119–143.

Carr, T. D., T. E. Williamson, B. B. Britt and K. Stadtman. 2011. Evidence for high taxonomic and morphometric tyrannosauroid diversity in the Late Cretaceous (Late Campanian) of the American Southwest and a new short-skulled tyrannosaurid from the Kaiparowits Formation of Utah. Naturwissenschaften doi:10.1007/s00114-011-0762-7.

Carrano, M. T., and J. R. Hutchinson. 2002. Pelvic and hindlimbs musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). Journal of Morphology 253: 207–228.

Carrano, M. T., J. R. Hutchinson and S. D. Sampson. 2005. New information on *Segisaurus halli*, a small theropod dinosaur from the Early Jurassic of Arizona. Journal of Vertebrate Paleontology 25: 835–849.

Cifelli, R., J. I. Kirkland, A. Weil, A. L. Deino and B. Kowallis. 1997. High-precision 40Ar/39Ar geochronology and the advent of North America' s Late Cretaceous terrestrial fauna: Proceedings of the Natural Academy of Science USA 94: 11163–11167.

Cifelli, R., R. L. Nydam, J. D. Gardner, A. Weil, J. G. Eaton, J. I. Kirkland and S. K. Madsen. 1999. Medial Cretaceous vertebrates from the Cedar Mountain Formation, Emery County, Utah: the Mussentuchit local fauna; pp. 219–242 *in* Gillette, D. D., (ed.), Vertebrate paleontology in Utah. Salt Lake City, Utah. Utah Department Natural Resources.

Curran, H. A. 1985. The trace fossil assemblage of a Cretaceous nearshore environment: Englishtown Formation of Delaware, U.S.A.; pp. 261–276 *in* Curran, H. A., (ed.), Biogenic Structures. Society of Economic Paleontologists and Mineralogists Special Publication 35, Tulsa.

Currie, P. J. 2003. Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. Acta Palaeontologica Polonica 48:191–226.

Currie, P. J. 2005. Theropods, including birds; pp. 367–397 *in* Currie, P. J., and Koppelhus, E. B., (eds.), Dinosaur Provincial Park, A Spectacular Ecosystem Revealed. Indiana University Press, Bloomington and Indianapolis, Indiana.

Dalman, S. G., A. K. Cantrell, T. L. Suazo and S. G. Lucas. 2016. First record of a tyrannosaurid theropod (Dinosauria) from the lower Campanian Menefee Formation, New Mexico. New Mexico Geological Society Proceedings Volume, 2016 Annual Spring Meeting, Macey Center, New Mexico Tech, Socorro, NM, p. 16A.

Dalman, S. G., and S. G. Lucas. 2015. New data on the tyrannosaurid theropods from the middle Campanian lower Judith River Formation of north-central Montana; pp. 77– 89 *in* Sullivan, R. M., and Lucas, S. G., (eds.), Fossil Record 4. New Mexico Museum of Natural History and Science Bulletin 67.

Dalman, S. G., and S. G. Lucas. 2016. Tyrannosaurid teeth from the Claggett Formation of the Elk Basin, Late Cretaceous of Western North America; pp. 83–89 *in* Khosla, A., and Lucas, S. G., (eds.), Cretaceous Period: Biotic Diversity and Biogeography. New Mexico Museum of Natural History and Science Bulletin 71.

Eaton, J. G., R. L. Cifelli, J. H. Hutchinson, J. I. Kirkland and J. M. Parrish. 1999. Cretaceous vertebrate faunas from the Kaiparowits Plateau, South- Central Utah; pp. 345–353 *in* Gillette, D. D., (ed.), Vertebrate paleontology in Utah. Salt Lake City, Utah. Utah Department Natural Resources.

Fiorillo, A. R., and R. S. Tykoski. 2014. A diminutive new tyrannosaur from the top of the world. PLOS ONE 9: e91287.

Gallagher, W. B. 1993. The Cretaceous/Tertiary mass extinction event in the northern Atlantic Coast Plain. The Mosasaur 5: 75–154.

Gallagher, W. B. 2004. Late Cretaceous dinosaurs from New Jersey and Delaware: stratigraphy, taphonomy and depositional environments. Geological Society of America, Abstracts with

Programs 36: 117A.
Gallagher, W. B. 2005. Recent mosasaur discoveries from New Jersey and Delaware, USA: stratigraphy, taphonomy and implications for mosasaur extinction. Netherlands Journal of Geosciences 84: 241–245.
Garrison, R. Jr., D. Brinkman, D. J. Nichols, P. Layer, D. Burge, D. Thayn. 2007. A multidisciplinary study of the Lower Cretaceous Cedar Mountain Formation, Mussentuchit Wash, Utah: a determination of the paleoenvironment and paleoecology of the *Eolambia caroljonesa* dinosaur quarry. Cretaceous Research 28: 461–494.
Hattori, S. 2016. Evolution of the hallux in non-avian theropod dinosaurs. Journal of Vertebrate Paleontology 36: e1116995.
Holtz, T. R. Jr. 1994. The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). Journal of Vertebrate Paleontology 14: 480–519.
Horner, J. R. 1979. Upper Cretaceous dinosaurs from the Bearpaw Shale (Marine) of south-central Montana with a checklist of Upper Cretaceous dinosaur remains from marine sediments in North America. Journal of Paleontology 53: 566–577.
Kirkland, J. I., B. Britt, D. L. Burge, K. Carpenter, R. Cifelli, F. DeCourten, J. Eaton, S. Hasiotis and T. Lawson. 1997. Lower to Middle Cretaceous dinosaur faunas: a key to understanding 35 million years of tectonics, evolution, and biogeography. Brigham Young University Geological Study 42: 69–103.
Krumenacker, L. J., D. Jade Simon, G. Scofield and D. J. Varricchio. 2016. Theropod dinosaurs from the Albian-Cenomanian Wayan Formation of eastern Idaho. Historical Biology 29: 170–186.
Larson, D. W. 2008. Diversity and variation of theropod dinosaur teeth from the uppermost Santonian Milk River Formation (Upper Cretaceous), Alberta: a quantitative method supporting identification of the oldest dinosaur tooth assemblage in Canada. Canadian Journal of Earth Sciences 45: 1455–1468.
Lauginiger, E. M. 1988. Cretaceous fossils from the Chesapeake and Delaware Canal: a guide for students and collectors. Delaware Geological Survey, Special Publication 18: 1–61.
Lehman, T. M., and S. T. Wick. 2012.Tyrannosauroid dinosaurs from the Aguja Formation (Upper Cretaceous) of Big Bend National Park, Texas. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 103: 1–15.
Loewen, M. A., R. B. Irmis, J. W. Sertich, P. J. Currie and S. D. Sampson. 2013. Tyrant dinosaur evolution tracks the rise and fall of Late Cretaceous oceans. PLOS ONE 8: e79420.
Marsh, O. C. 1877. Notice of a new gigantic dinosaur. American Journal of Science 114: 87–88.
Marsh, O. C. 1881. Principal characters of American Jurassic dinosaurs Part V. American Journal of Science, Series 3, 21: 417–423.
Osborn, H. F. 1916. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. Bulletin of the American Museum of Natural History 35: 733–771.
Osmólska, H., E. Roniewicz and R. Barsbold. 1972. A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. Palaeontologica Polonica 27: 103–143.
Owen, R. 1842. Report on British Fossil Reptiles. Part II. Reports of the British Association for the Advancement of Science 11: 60–204
Owens, J. P., J. P. Minard, N. F. Sohl and J. F. Mello. 1970. Stratigraphy of the outcropping post-Magothy Upper Cretaceous formations in southern New Jersey and northern Delmarva Peninsula, Delaware and Maryland. United States Government Printing Office, Washington, 60 pp.
Parrish, J. M. 1999. Dinosaur teeth from the Upper Cretaceous (Turonian–Judithian) of southern Utah; pp. 319–321 *in* Gillette, D. D., (ed.), Vertebrate Paleontology in Utah. Salt Lake City, Utah. Utah Department Natural Resources.
Peecook, B. R., J. A. Wilson, R. Hernández-Rivera, M. Montellano-Ballesteros and G. P. Wilson. 2014. First tyrannosaurid remains from the Upper Cretaceous "El Gallo" Formation of Baja California, Mexico. Acta Palaeontologica Polonica 59: 71–80.
Petters, S. W. 1976. Upper Cretaceous subsurface stratigraphy of Atlantic Coastal Plain of New Jersey. American Association of Petroleum Geologists Bulletin 60: 87–107.
Ramsey, K. W. 2005. Geologic map of New Castle County, Delaware: Delaware Geological Survey, University of Delaware, Newark, DE.
Robb, A. J., III. 2004. Vertebrate fossils from the Upper Cretaceous (Merchantville Formation: early Campanian) Graham Brick Yards locality of New Jersey. The Mosasaur 7: 75–88.
Russell, D. A. 1970. Tyrannosaurs from the Late Cretaceous of western Canada. National Museum of Natural Science, Publications in Paleontology 1: 1–34.
Schwimmer, D. R. 1989. First dinosaur fossils from Georgia, with notes on additional Cretaceous vertebrates from the state. Faculty Bibliography. Paper 463: 147–157pp.
Schwimmer, D. R. 2004. Late Cretaceous dinosaurs of the eastern Gulf Coast, and their relationships with Atlantic Coast taxa. Geological Society of America, Abstracts with Programs 36: 117A.
Schwimmer, D. R., G. Dent Williams, J. L. Dobie and W. G. Siesser. 1993. Late Cretaceous dinosaurs from the Blufftown Formation in western Georgia and eastern Alabama. Journal of Paleontology 67: 288–296.
Serrano-Brañas, C. I., C. Gutiérrez-Blando, R. Duarte Bigurra and C. M. González-León. 2017. First occurrence of tyrannosaurid theropods from the Corral de Enmedio Formation (Upper Cretaceous) Sonora, México. Cretaceous Research 75: 81–93.
Snively, E., and A. P. Russell. 2002. The tyrannosaurid metatarsus: bone strain and inferred ligament function. Senckenbergiana Lethaea 81: 73–80.
Snively, E., A. P. Russell and G. L. Powell. 2004. Evolutionary morphology of the coelurosaurian arctometatarsus: descriptive, morphometric and phylogenetic approaches. Zoological Journal of the Linnean Society 142: 525–553.
Tarsitano, S. F., and M. K. Hecht. 1980. A reconsideration of the

reptilian relationships of *Archaeopteryx*. Zoological Journal of the Linnean Society 69: 149–182.

Thompson, T. J., R. B. Irmis, and M. A. Loewen. 2013. First occurrence of a tyrannosaurid dinosaur from the Mesaverde Group (Neslen Formation) of Utah: Implications for upper Campanian Laramidian biogeography. Cretaceous Research 43: 70–79.

von Huene, F. R. 1914. Das natürliche System der Saurischia. Zentralblatt für Mineralogie, Geologie, und Paläontologie B 1914: 154–158.

Walker, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. Philosophical Transactions of the Royal Society of London, B, 248: 53–134.

Weishampel, D. B. 2004. History and significance of East Coast dinosaurs. Geological Society of America, Abstracts with Programs 36: 95A.

Weishampel, D. B. 2006. Another look at the dinosaurs of the East Coast of North America. Actas de las III Jornadas sobre Dinosaurios y su Entorno: 129–168.

Weishampel, D .B., P. M. Barret, R. A. Coria, J. Le Loeuff, X. Xu, X. Zhao, A. Sahni, E. M. P. Gomani and C. R. Noto. 2004. Dinosaur distribution; pp. 517–606 *in* Weishampel, D. B., Dodson, P., and Osmólska, H., (eds.), The Dinosauria, 2nd edition.

Wick, S. L., T. M. Lehman and A. A. Brink. 2015. A theropod tooth assemblage from the lower Aguja Formation (early Campanian) of West Texas, and the roles of small theropod and varanoid lizard mesopredators in a tropical predator guild. Palaeogeography, Palaeoclimatology, Palaeoecology 418: 229–244.

Zanno, L. E., and P. J. Makovicky. 2011. On the earliest record of Cretaceous tyrannosauroids in western North America: implications for an Early Cretaceous Laurasian interchange event. Historical Biology: 3952.

APPENDIX 1

Anatomical Abbreviations

dlr, distolateral ridge; **dt4**, articulation for distal tarsal 4; **gls**, M. gastrocnemius pars lateralis insertion scar; **hp**, hyperextensor pit; **lc**, lateral condyle; **llf**, lateral ligament fossa; **llp**, lateral ligament pit; **lnIII**, lateral notch for the articulation with the "L" – shaped proximal articular end of metatarsal III; **mV**, contact with metatarsal V; **mc**, medial condyle; **mlf**, medial ligament fossae; **mlp**, medial ligament pit; **mnIII**, medial notch for the articulation with the "L" – shaped proximal articular end of metatarsal III; **mt-I**, metatarsal I articular surface; **M. ta**, M. tibialis anterior; **mt-I**, metatarsal I articular surface; **pmr**, posteromedial ridge.