

A Tyrannosauroid Metatarsus from the Merchantville Formation of Delaware increases the diversity of non-Tyrannosaurid Tyrannosauroids on Appalachia

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Abstract.

For almost the entirety of the latter half of the Cretaceous, the continent of North America was divided into two sections, Laramidia in the west and Appalachia in the east.

Though/Although the

depositional environments of Appalachia recorded only a sparse fossil record of dinosaurs, the dinosaur faunas were different in composition from those of Laramidia. Represented by at least two taxa (*Appalachiosaurus montgomeriensis* and *Dryptosaurus aquilunguis*), partial and fragmentary skeletons, and isolated bones, the non-tyrannosaurid tyrannosauroids of the landmass have attracted some attention. Unfortunately, these eastern tyrants are poorly known compared to their western contemporaries. Here, one specimen, the partial metatarsus of a tyrannosauroid from the Campanian Merchantville Formation of Delaware, is described in detail. The specimen can be distinguished from *Appalachiosaurus montgomeriensis* and *Dryptosaurus aquilunguis* by several morphological differences. As such, the specimen represents a potentially previously unrecognized new taxon of tyrannosauroid from Appalachia, increasing the diversity of the clade on the landmass. Phylogenetic analysis and the morphology of the bones suggest the Merchantville specimen is a tyrannosauroid of “intermediate” grade, thus supporting the notion that Appalachia was a refugium for relict dinosaur clades.

Introduction.

The fossil record of Appalachia, a landmass formed ~~in~~from the eastern half of North America by the ~~creation~~expansion of the Western Interior Seaway (e.g., Russell, 1995; Roberts & Kirschbaum, 1995; Lehman, 1997; Schwimmer, 1997; Schwimmer, 2002), is poor in contrast to that of Cretaceous-aged western North America (Laramidia), with dinosaurs only represented by isolated elements, ~~fragmentary~~, and ~~occasionally~~rare partial skeletons (e.g., Gallagher, 1993; Schwimmer, 1997; Ebersole & King, 2011). Nevertheless, the dinosaur faunas of Appalachia have come to light gradually, consisting of hadrosauroids, hadrosaurids, nodosaurids, leptoceratopsians, indeterminate ornithopods, dromaeosaurids, ornithomimosaurs, indeterminate maniraptorans, and non-tyrannosaurid tyrannosauroids (e.g., Gallagher, 1993; Schwimmer, 1997; Schwimmer, 2002; Ebersole & King, 2011; Schwimmer et al., 2015; Longrich, 2016). The tyrannosauroid taxa of this landmass, *Dryptosaurus* and *Appalachiosaurus*, have been ~~found~~placed outside Tyrannosauridae in multiple phylogenetic analyses (e.g., Holtz, 2004; Carr, Williamson & Schwimmer, 2005; Brusatte et al., 2010; Brusatte, Benson & Norell, 2011; Loewen et al., 2013; Fiorillo & Tykoski, 2014; Brusatte & Carr, 2016; Brusatte et al., 2016; Carr et al., 2017). Brusatte & Carr (2016) also found *Dryptosaurus aquilunguis* as an Alioramine tyrannosauroid in their Bayesian analysis, though this result has not been corroborated by a more recent parsimony analysis of Tyrannosauroidea using the same dataset with additional taxa and added characters (e.g., Carr et al., 2017). The fossil record of tyrannosauroids from Appalachia is limited to the holotypes of *Dryptosaurus* and *Appalachiosaurus*, undescribed partial specimens, and isolated bones and teeth, limiting our understanding of these animals. Overall, the scarcity of tyrannosauroid specimens from

Appalachia means that the description of additional specimens and their inclusion in phylogenetic analysis is needed to better illuminate the understanding of the diversity, biogeography, and evolutionary position of the eastern tyrant dinosaurs.

One productive area for Late Cretaceous dinosaur specimen in eastern North America is the portion of the Atlantic Coastal Plain that includes New Jersey and Delaware (e.g., Gallagher, 1993). Cretaceous sediments in this area range from the Cenomanian to the Maastrichtian stages of the Late Cretaceous (e.g., Miller et al., 2004). In this paper, the partial metatarsus of a tyrannosauroid from the early Campanian Merchantville Formation of Delaware is described, assignable to that clade based on the morphology of the proximal articular surfaces of metatarsals II and IV indicating a proximally crescentic metatarsal III that was restricted to the plantar surface of the proximal end of the metatarsus, an autapomorphy of the group (Holtz, 2004; see below). The specimen, YPM VPPU.021795, can be distinguished from *Appalachiosaurus montgomeriensis* (Carr, Williamson & Schwimmer, 2005) and *Dryptosaurus aquilunguis* (e.g., Brusatte, Benson & Norell, 2011) by a variety of morphological features. Thus, it potentially represents a new previously unrecognized taxon of tyrannosauroid from Appalachia, adding diversity to the clade in the Campanian of eastern North America. Both the results from phylogenetic analysis and the presence of several features on YPM VPPU.021795 strongly support a position outside of Tyrannosauridae for the specimen, further evincing the presence of “intermediate” tyrannosauroids on Appalachia (e.g., Carr, Williamson & Schwimmer, 2005; Brusatte, Benson & Norell, 2011) and providing additional evidence that at least some Appalachian dinosaurs represent relict forms that survived on the landmass into the Late Cretaceous (e.g., Schwimmer, 1997).

Methods.

Permits.

No permits were required for this study, which complied with all relevant regulations.

Access to the collections at the American Museum of Natural History was provided by Carl Mehling, whereas access to the collections at the Yale Peabody Museum was provided by Daniel Brinkman.

Institutional Abbreviations.

~~The term “AMNH FARB” is used to refer to the~~ fossil amphibian, reptile and bird collections of the American Museum of Natural History ~~in~~, New York, NY; ROM: Royal Ontario Museum, Toronto, ON, Canada; ~~and the term “YPM VPPU” is used to refer to the vertebrate paleontology collections of the; vertebrate paleontology collections, Yale Peabody Museum of Natural History, ~~in~~ New Haven, CT. ~~“ROM” is used to refer to the collections of the Royal Ontario Museum in Toronto, ON.~~~~

Photography.

The specimens described herein were photographed using a Canon Powershot G-12 digital camera and cropped using Apple Preview.

Phylogenetic analysis.

YPM VPPU.021795 was included in both the latest ~~addition~~published version of the Theropod Working Group matrix (Brusatte et al., 2014) to statistically test the placement of the specimen in Coelurosauria and the matrix of Carr et al. (2017) to better resolve the placement of YPM VPPU.021795 within Tyrannosauroidae. The matrices were entered into TNT v. 1.5 in the command.tnt line in an analysis of parsimony (Goloboff & Catalano, 2016). In order to make the analysis of YPM VPPU.021795 in the matrices of Brusatte et al. (2014) and Carr et al. (2017)

comparable to the protocols of those studies, the author followed the first's procedure of using *Allosaurus* and the second's of using *Allosaurus* sp., Maniraptora, Ornithomimosauria, and *Compsognathus longipes* as outgroup taxa. As in Carr et al. (2017), *Raptorex* was regarded as a juvenile

tyrannosaurine and excluded from the analysis, and *Alioramus altai* and *A. remotus* were entered into the program as one taxon. The "New Technology Search" was used in both analyses with default parameters for the options of sectorial search, ratchet, tree drift, and tree fuse.

For the analysis of YPM VPPU.021795 within the matrix of Carr et al. (2017), 32 most parsimonious trees (MPTs) were recovered, whereas in the analysis in the Theropod Working Group matrix, 81 were found. These trees were then subjected to traditional TBR branch swapping, which

recovered no additional MPTs. Clade support was then quantified by use of bootstrap values (100 replicates; Goloboff & Catalano, 2016). Finally, the MPTs were summarized in a 50% majority rule tree for both analyses, yielding slightly different topologies in either case.

Results.

Geological Setting.

YPM VPPU.021795 is an associated specimen collected by Ralph Johnson and Ray Meyer of the Monmouth Amateur Paleontologist's Society from a single outcrop of the Merchantville Formation exposed at low tide along a portion of the southern bank of the Chesapeake and Delaware Canal approximately 0.75 miles east of Summit Bridge (Route 301) and 0.5 miles north of Summit, Delaware. Both metatarsals are reddish-brown in color, similar in

length (Table 1) and both from the left pes of a theropod, both of similar preservation (Figs. 1-2), both individually assignable to tyrannosauroids, and were found associated in the same deposit, indicating they belong to the same individual.

Gallagher (1993) described the Merchantville Formation as consisting of black to dark greenish-gray micaceous, silty clay to fine sand, noting its early Campanian age. Miller et al. (2004) found the Merchantville Formation to be latest Santonian to early Campanian in age (84.3-77.8 Ma), seated within the Merchantville Sequence, and to be consisting of glauconite sands and glauconitic clays. In addition to the tyrannosauroid YPM VPPU.021795, tetrapods known from the Merchantville Formation include crocodylians, the mosasaurs *Clidastes iguanavus* and *Halisaurus platyspondylus*, the turtles *Bothremys cooki* and *Trionyx halophila*, the dinosaur *Hadrosaurus foulkii*, a specimen comparable to *Dryptosaurus*, and indeterminate ornithomimosaur and hadrosaur (Gallagher, 1993; Weishampel & Young, 1996).

At the site of discovery, the Chesapeake and Delaware Canal, Baird & Galton (1981) described the Merchantville Formation as a deposit consisting of silty and clayey glauconitic and micaceous thick-bedded sand of a thickness of approximately 23 feet, describing pterosaur specimens from the site as well as noting the presence of fossils of the turtle *Toxochelys*, the mosasaur *Tylosaurus*, and a hadrosaurid dinosaur remains nearby.

Systematic Paleontology.

Dinosauria Owen (1842) sensu Padian & May (1993)

Theropoda Marsh (1881) sensu Gauthier (1986)

Coelurosauria Huene (1914) sensu Sereno et al. (2005)

Tyrannosauroida Osborn (1905) sensu Holtz (2004)

Tyrannosauroida indet.

Material: YPM VPPU.021795, partial left metatarsals II and IV of a tyrannosauroid dinosaur.

Referral to Tyrannosauroidea: The specimen YPM VPPU.021795 is referred to a tyrannosauroid based on several features that unite the specimen with that clade and larger, more inclusive ones within Theropoda. The presence of developed buttressing surfaces and proximal articular facets on each of the two preserved metatarsals (Fig. 1, Fig. 2) unite YPM VPPU.021795 with

Arctometatarsalia (e.g., Holtz, 1994). In YPM VPPU.021795, the proximal articular surface of metatarsal IV appears as a deep, V-shaped notch on the medial surface of the bone that articulated with the lateral surface of the proximal end of a crescentic metatarsal III to form an arctometatarsus where the metatarsals were closely appressed (Fig. 2B, E), a morphology autapomorphic to Tyrannosauroidea (e.g., Holtz, 2004; Thompson, Irmis & Loewen, 2013; character 423 in Brusatte et al. 2014; Peacock et al., 2004). The buttressing surfaces on the medial face of metatarsal IV and the lateral surface of metatarsal II of YPM VPPU.021795 are large and teardrop-shaped, ~~further uniting the bones with~~ another similarity with the condition in Tyrannosauroidea (e.g., character 303 in Brusatte et al., 2010; Thomson, Irmis & Loewen, 2013; Peacock et al., 2014; character 303 in Brusatte & Carr, 2016). All of these features have previously been used to assign the isolated metatarsals and fragmentary hindlimbs of arctometatarsalian theropods to Tyrannosauroidea (Thomson, Irmis & Loewen, 2013; Peacock et al., 2014), so this assignment is not without methodical precedent. The proximal articular surface for metatarsal III on metatarsals IV and II is also found in arctometatarsalian ornithomimosaurs, caenagnathids, and troodontids (e.g., Holtz, 1994), and as such rejection of the assignment of YPM VPPU.021795 to these groups is discussed below.

Ornithomimids share several features in their metatarsals with tyrannosauroids, and as Baird & Galton (1981) assigned YPM VPPU.021795 to an ornithomimosaur, explicit rejection

of the alternative hypothesis that YPM VPPU.021795 belongs to an ornithomimosaur is especially warranted. In arctometatarsalian ornithomimosaur, the proximal articular facets on metatarsals II and IV for metatarsal III are poorly developed and shallow to accommodate a proximally ovoid metatarsal III (e.g., Osborn, 1921; Osmólska, Roniewicz & Barsbold, 1972; Barsbold & Osmólska, 1990; Shapiro et al., 2003; Makovicky, Kobayashi & Currie, 2004; Xu et al., 2011; Brusatte et al., 2012; Cullen et al., 2013; Peacock et al., 2014; McFeeters et al., 2016; Sues & Averianov, 2016; Tsogtbaatar et al., 2017). This morphology is not seen in YPM VPPU.021795, where the proximal articular facet of metatarsal IV shows that the bone articulated with a proximally crescentic metatarsal III, autapomorphic [offor](#) Tyrannosauroidae (Fig. 2E; Holtz, 2004). This indicated shape for metatarsal III also distinguishes it from the other arctometatarsalian groups noted above, as does the size of YPM VPPU.021795 from referral to Troodontidae (e.g., Makovicky & Norell, 2004; Peacock et al., 2014). The preserved bone surface of metatarsal IV in YPM VPPU.021795 indicates a lateral divergence of metatarsal IV distally that further distinguishes the specimen from ornithomimosaur and caenagnathids (e.g., character 302 in Brusatte et al., 2010; Peacock et al., 2014; character 302 in Brusatte & Carr, 2016).

[_____](#) The lack of a deep proximal articular facet on the metatarsal II included in YPM VPPU.021795 as preserved warrants rigorous comparison of this bone with the [metatarsal equivalent elements](#) of arctometatarsalian ornithomimosaur, where the condition is somewhat similar (e.g., Makovicky, Kobayashi & Currie, 2004; Brusatte et al., 2012).

Nevertheless, several features of the metatarsal II suggest the bone came from a tyrannosauroid. Factoring in the clear damage and deformation of the bone (Fig. 1), the presence of a deepened facet on the medial surface of metatarsal II between the proximal articular surface and

buttressing surface for metatarsal III suggests that a deeper proximal articular facet was once present (Fig. 1B-C, E). The presence of a large, teardrop-shaped buttressing surface for metatarsal III on this bone also allies this specimen with Tyrannosauroida (e.g., Holtz, 2004; Thomson, Irmis & Loewen, 2013; Loewen et al., 2013). The medial extension outward of the Merchantville metatarsal II proximally as indicated by the preserved bone (Fig. 2C) does not match the condition in ornithomimosaurs, as because in arctometatarsalian ornithomimosaurs the medial divergence proximally of metatarsal II is not sharply divergent from the shaft if present at all (e.g., Fig. 3A1, C in Osborn, 1921; Fig. 16A1 in Osmólska, Roniewicz & Barsbold, 1972; Fig. 6A in Xu et al., 2011; Fig. 10F, J in McFeeters et al., 2016; Fig. 21B in Sues & Avarianov, 2016). This morphology more closely matches the metatarsals II of tyrannosauroids (e.g., Fig. 44A in Lambe, 1917; Fig. 1 in Currie, 1998; Fig. 19C in Carr, Williamson & Schwimmer, 2005).

 The size and elongate morphology of the Merchantville metatarsal II is also at odds with the metatarsals of the other known theropod taxa of Appalachia, including those of dromaeosaurids (e.g., Keirnan & Schwimmer, 2004; Ebersole & King, 2011; Schwimmer et al., 2015), which are proximodistally robust and not arctometatarsalian (e.g., Norell & Makovicky, 2004). Finally, the association and comparability of this bone with the metatarsal IV described herein that clearly bears the deep, sharply pointed notch for the articulation with a crescentic metatarsal III autapomorphic for Tyrannosauroida (Holtz, 2004) warrant its assignment to that clade.

Finally, YPM VPPU.021795 was placed in the phylogenetic matrix of Brusatte et al. (2014) to phylogenetically test the relationships of YPM VPPU.021795 among Coelurosauria and was found to be the basalmost tyrannosauroid in the strict consensus tree (tree length = 3250,

consistency index = 0.333, retention index = 0.788). The 50% majority rule tree topology shows the Merchantville specimen as an outgroup to all other coelurosaurs along with basal forms like *Tugulosaurus* and the Tyrannosauroidae. Thus, there is certainly broader phylogenetic support for the referral of YPM VPPU.021795 into Tyrannosauroidae.

Description.

Metatarsal II.

The proximal two thirds of the left metatarsal II (Fig. 1A-F) is eroded, though the dorsal surface is smooth and partially intact. Measurements of the specimen are in Table 1. The distal end of the preserved portion of metatarsal II is heavily eroded and apparently deformed from compression, curving laterally towards its distal end. Nevertheless, the insertion scar for the M. gastrocnemius pars lateralis is preserved as a slight, linear fossa on the proximal end of the medial surface of this bone (Fig. 1B)(Carrano & Hutchinson, 2002). The proximal articular surface for metatarsal III appears as a ventrolaterally oriented shallow notch. However, the proximal end of this bone is heavily reconstructed (especially at the dorsal end of the proximal surface, Fig. 1C) and seems to have undergone ~~water-wear~~abrasion and deformation. The proximal articular facet for metatarsal III seems have been somewhat more developed (Fig. 1E), though the preserved bone surface indicates a notch less prominent than in *Appalachiosaurus* and other taxa (Fig. 1E; Table 2; see discussion below). The bulbous morphology of the proximal end may be a taphonomic artifact from transport out to sea as well as from the stabilization of this bone during preparation. Across the lateral face of metatarsal II, a subtle but dorsoventrally elongate buttressing surface like that observed in the metatarsal II of *Appalachiosaurus* (e.g., Carr, Williamson & Schwimmer, 2005) begins 50 mm below the lateral facet for metatarsal III and extends downward the shaft, being cut off at the clean break at the distal end of the

specimen. The preserved bone of the dorsal half of the proximal end extends medially outward from the shaft 17 mm dorsally, whereas ventrally it only does so by 9 mm. The metatarsal II seems to have been more robust than the metatarsal IV included in YPM VPPU.021795 when uncrushed, as found in other tyrannosauroids (e.g., Holtz, 2004).

Metatarsal IV.

The proximal two thirds of the left metatarsal IV (Fig. 2A-F) is the best preserved portion of the two bones, with little indication of crushing along its shaft. Towards the bottom of its dorsal surface, the specimen preserves scrapes that are consistent with evidence of shark scavenging (Fig. 2C) found in other specimens of dinosaur from the Atlantic Coastal Plain (e.g., Schein & Poole, 2014). This evidence of feeding activity by sharks suggests the metatarsus floated out to sea before it was deposited. The lateral surface is smooth, with a noticeable ventral edge that is almost kinked at a right angle (Fig. 2A). The dorsal surface is smooth and convex, expanding mediolaterally and dorsoventrally outward towards the proximal end of the specimen. The ventral surface, which is flattened, mirrors the dorsal surface in its expansion. The medial surface is very flattened at the shaft, except for two ridges that extend diagonally from the ventral edge of the medial and lateral surfaces approximately 2 mm above the diaphysis to the dorsal edge of the medial and lateral surfaces at its distal end. These form a dorsoventrally elongate, teardrop-shaped buttressing surface for the articulation with metatarsal III (Fig. 2B), a feature found in other arctometatarsalian tyrannosauroids (e.g., Thomson, Irmis & Loewen, 2013; Loewen et al., 2013; Peacock et al., 2014; Brusatte & Carr, 2016). The elliptical insertion point for the M. tibialis anterior (Carrano & Hutchinson, 2002) is faded, but present and undeformed (Fig. 2B). The presence of the undistorted buttressing surface on the medial side with clear borders indicates the bone was not mediolaterally compressed from taphonomy. The

proximal expansion of the medial side of metatarsal IV has the clear medial articular facet for metatarsal III found in *Appalachiosaurus*, *Dryptosaurus*, and tyrannosaurids (e.g., Holtz, 2004; Carr, Williamson & Schwimmer, 2005; Brusatte, Benson & Norell, 2011). This morphology indicates the autapomorphy of Tyrannosauroidae of a proximally crescentic metatarsal III that is limited to the plantar half of the proximal face of the metatarsus (Holtz, 2004). The insertion for the M.

gastrocnemius lateralis (Carrano & Hutchinson, 2002) is poorly visible due to erosional damage, though it may still be preserved towards the far distal end of the proximal portion of the preserved metatarsal IV (Fig. 2D). Between the articular surface for the metatarsal III on the medial surface and the insertion point for the M. gastrocnemius lateralis, the shaft of the metatarsal IV is flattened. Previously, this feature has been used to distinguish between arctometatarsalian non-tyrannosaurid tyrannosauroids and the clade Tyrannosauridae (e.g., Peacock et al., 2014).

The distal ~~sixth~~end of the metatarsal IV was also preserved, though it was separated from the main portion of this metatarsal. The measurements of this specimen are included in Table 1.

The distal end of metatarsal IV is semi-rectangular rather than triangular in shape and has a subtle sulcus separating the distal hemicondyles (Fig. 2F). The medial face is flattened in distal view, though this may be an artifact of preservation. In lateral and medial views, the distal end is very heavily eroded, especially proximally. The medial collateral ligament pit is semi-ovoid and deeper than the lateral collateral ligament pit. Between this distal end and the proximal portion, the metatarsal is approximately four-fifths complete based on the completeness of the buttressing surface for metatarsal III on the medial face. The estimated length of this metatarsal when

complete is 464 mm long proximodistally, approximately the same size as the metatarsal IV of *Appalachiosaurus montgomeriensis* (Carr, Williamson & Schwimmer, 2005).

Discussion.

Comparisons with other tyrannosauroids.

YPM VPPU.021795 can be confidently assigned to a tyrannosauroid dinosaur based on the presence of an arctometatarsalian metatarsus with a proximally crescentic metatarsal III that closely articulates with a metatarsal IV with a deep, sharply notched proximal articular facet, a metatarsal II with a notch that also indicates close articulation with metatarsal III, the presence of large, dorsoventrally elongate, teardrop-shaped buttressing surfaces on both bones for the articulation with metatarsal III, and a laterally divergent metatarsal IV proximally (e.g., Holtz, 2004; Brusatte et al., 2010; Loewen et al., 2013; Thomson, Irmis & Loewen, 2013; Peacock et al., 2014; Brusatte & Carr, 2016).

Tyrannosauroids increased in size from the Middle Jurassic to the Late Cretaceous, the clade eventually giving rise to massive terrestrial predators like *Albertosaurus sarcophagus*, *Dryptosaurus aquilunguis*, and *Tyrannosaurus rex* (e.g., Xu et al., 2010; Holtz, 2012; Peacock et al., 2014; Brusatte et al., 2016). YPM VPPU.021795 clearly belongs among the ranks of the larger species of the Late Cretaceous based on the length of the metatarsals when compared to those of earlier forms (e.g., Peacock et al., 2014). ~~To further analyze the position of the specimen in Tyrannosauroidae as well as to provide statistical support for the inclusion of the specimens in the clade, YPM VPPU.021795 was coded and included in the matrix of Carr et al. (2017) in addition to being included in the Theropod Working Group matrix (TWiG) (Brusatte et al., 2014).~~ Previous studies on fragmentary or isolated tyrannosauroid postcranial specimens have noted the

lack of characters from the metatarsus in matrices which encompass Tyrannosauroida (e.g., Peacock et al., 2014), with some studies on fragmentary hindlimb material not performing a phylogenetic analysis at all (e.g., Thomson, Irmis & Loewen, 2013). Indeed, only 5 of the 386 characters (~1.3%) included in the matrix of Carr et al. (2017) could be coded using YPM VPPU.021795. The characters scored were 377[1], 380[1], 381[0], 383[1], and 384[0], and the matrix was analyzed using TNT v.1.5 (Goloboff & Catalano, 2016). The tyrannosauroid represented by YPM VPPU.021795 was found to be an intermediate-grade tyrannosauroid closely related to *Timurlengia*, *Appalachiosaurus*, *Dryptosaurus*, and the Iren Dabasu tyrannosauroid in each of the 32 most parsimonious trees (MPTs) found (tree length = 782, consistency index = 0.574, retention index = 0.49), the strict consensus placing the Merchantville specimen as an outgroup to the clade containing *Bistahieversor* and Tyrannosauridae along with *Dryptosaurus*, *Appalachiosaurus*, *Xiongguanlong*, *Timurlengia*, and the Iren Dabasu taxon and the 50% majority rule tree placing the Merchantville taxon alongside *Dryptosaurus* and the clade including *Timurlengia* and the Iren Dabasu taxon as a sister taxon to *Appalachiosaurus* and more derived tyrannosauroids.

A position outside Tyrannosauridae for YPM VPPU.021795 is also supported by several features outside those coded. For example, the portion of bone between the medial buttressing surface for metatarsal III and the insertion point for the M. gastocnemius lateralis is flattened, unlike the concave condition found in tyrannosaurids (e.g., Peacock et al., 2014). To compare YPM VPPU.021795 proportionally with other tyrannosauroids, the robusticity index (RI) used in Peacock et al. (2014) was employed. The RI is equal to the ratio of the circumference at the

diaphysis to the proximodistal length of a metatarsal IV (Peacock et al., 2014). The RI for YPM VPPU.021795 (Table 1) was calculated as 0.2823, appreciably smaller than the indices for tyrannosaurids (0.3200+)(Peacock et al., 2014).

YPM VPPU.021795 was also compared with other metatarsals of tyrannosauroids from Appalachia. In proximal view, the expanded proximal end of the metatarsal II differs from the corresponding surface in the right metatarsal II of *Appalachiosaurus montgomeriensis* in that in *A. montgomeriensis*, a far deeper and sharper notch-like articular facet for metatarsal III is clearly present, even accounting for erosional damage and deformation on the Merchantville specimen (Fig. 1E; Fig. 19F in Carr, Williamson & Schwimmer, 2005). The metatarsal IV of YPM VPPU.021795 lacks the autapomorphic feature found in *Dryptosaurus aquilunguis* of having a shaft that in proximal view has a semiovoid cross-section significantly wider mediolaterally than dorsoventrally (Brusatte, Benson & Norell, 2011). Taphonomic deformation can be ruled out as the cause for this, as the proximal two-thirds of the metatarsal IV included in YPM VPPU.021795 show no indications of mediolateral compression from taphonomy. Rather, the proximal shape of this bone in the Merchantville specimen is typical of arctometatarsalian tyrannosauroids (e.g., cf. Fig. 19D in Carr, Williamson & Schwimmer, 2005; Fig. 3J in Thomson, Irmis & Loewen, 2013; Fig. 1E in Peacock et al., 2014). Additionally, the estimated length of the metatarsal IV of YPM VPPU.021795 when complete (Table 1) exceeds the length of the metatarsal IV included in the apparently adult or near-adult holotype specimen of *D. aquilunguis* by 73 mm (Brusatte, Benson & Norell, 2011).

In distal view (Fig. 2F), the metatarsal IV is notably different in morphology from the corresponding element in the holotype of *Appalachiosaurus montgomeriensis* or *Dryptosaurus aquilunguis* (Fig. 19G in Carr, Williamson & Schwimmer, 2005; Fig. 22F in Brusatte, Benson &

Norell, 2011). Unlike the condition in *A. montgomeriensis* or *D. aquilunguis*, the distal end of metatarsal IV is semi-rectangular rather than triangular in shape and is additionally differentiated from the former in having a more gently arched sulcus separating the distal hemicondyles (Fig. 19G in Carr, Williamson & Schwimmer, 2005). As no autapomorphies of *Appalachiosaurus* are found on the metatarsus, YPM VPPU.021795 cannot be confidently assigned to that taxon.

Several studies regarding the ontogeny of tyrannosauroid dinosaurs have noted that substantial changes in the skeleton of tyrannosauroid taxa, such as increasing robusticity of the hindlimbs, occurred during growth (e.g., Carr, 1999; Currie, 2003; Currie, Hurum & Sabath, 2003; Carr & Williamson, 2004; Carr, Williamson & Schwimmer, 2005; Peacock et al., 2014). However, ontogenetic variation contributing to these differences between YPM VPPU.021795, *Dryptosaurus aquilunguis*, and *Appalachiosaurus montgomeriensis* may be ruled out, as the estimated length of the Merchantville metatarsals when complete greatly exceed the dimensions of the corresponding bones of the holotype individual of *D. aquilunguis*, which is apparently an adult (Brusatte, Benson & Norell, 2011), suggesting YPM VPPU.021795 does not represent a growth stage of this taxon and differences between the two specimens are not from ontogeny. In *Dryptosaurus aquilunguis*, the metatarsal IV measures approximately 392 mm long (Brusatte, Benson & Norell, 2011; Peacock et al., 2014), whereas the estimated length of the Merchantville metatarsal IV is 72 mm longer at 464 mm (Table 1). Though metatarsal length does indeed vary in tyrannosauroids where multiple adult individuals are known (e.g., Peacock et al., 2014), the disparity in the lengths of the metatarsal IV of *Dryptosaurus* and that of YPM VPPU.021795 (by more than 10% of the length of the latter) along with the morphological differences between them suggest against these taxa being synonymous. The Merchantville bones do, however, nearly

match the dimensions in *Appalachiosaurus montgomeriensis* (Carr, Williamson & Schwimmer, 2005). This suggests against the hypothesis that the metatarsals represent a different ontogenetic stage of *Appalachiosaurus*, though size has been criticized as an indicator of ontogeny (e.g., Hone et al., 2016).

Individual variation is impossible to rule out, as both *Dryptosaurus* and *Appalachiosaurus* are poorly known outside the holotype specimens of each, making the sample size for each effectively one (e.g., Gallagher, 1993; Carr, Williamson & Schwimmer, 2005; Brusatte, Benson & Norell, 2011; Ebersole & King, 2011). One metatarsal IV from the Blufftown Formation has been referred to *Appalachiosaurus montgomeriensis* (Ebersole & King, 2011). Though the specimen as figured in Schwimmer et al. (1993) indeed resembles closely the metatarsal IV described herein, its estimated length (=440 mm)(Schwimmer et al., 1993) is smaller than that for the Merchantville bone by about 30 mm (Table 1). Ontogeny thus cannot be accounted for in this case due to the small sample size and fragmentary nature of the Merchantville specimen and the Blufftown metatarsus. In the same way, comparison of YPM VPPU.021795 with the smaller metatarsals included in AMNH 2550-2553, which represent a tyrannosauroid or ornithomimosaur, is not possible, though it should be noted that YPM VPPU.021795 and these AMNH specimens are separated by several million years (e.g., Miller et al., 2004). In the case of comparison between *Dryptosaurus aquilunguis* and YPM VPPU.021795, the lack of an autapomorphy of the former taxon on the latter specimen is considered beyond intraspecific variation and grounds for separating the two. However, the differences between YPM VPPU.021795 and *Appalachiosaurus*, which include the appreciable difference between their RI, differently shaped metatarsals IV distally, and the lack of a deepened proximal articular

facet for metatarsal III on the metatarsal II of the former taxon, could be from intraspecific variation and are discussed herein.

Schwimmer et al. (1993), Carr, Williamson & Schwimmer (2005), and Schwimmer (2017, pers. comm.) note that the metatarsals of *Appalachiosaurus* and the referred Blufftown specimen match the corresponding bones of *Gorgosaurus libratus* very closely. On the species level, individual tyrannosauroids have proportionally similar metatarsals when such bones are of the same or very similar length (e.g., Fig. 1 in Currie, 1998; Fig. 8.11 in Larson, 2008; Table 2, 3 in Peacock et al., 2014). For example, several metatarsals of similar length (= +/- 20 mm) assigned to *Albertosaurus* (AMNH FARB 5232, and AMNH FARB 5233, RIs 3513, 3568; AMNH FARB 5235 and ROM 807, RIs 0.3972, 0.4106) have RIs that differ by approximately 0.01 or less, much less than the difference in the RIs of *Appalachiosaurus* and the Merchantville taxon (0.6480) or between the latter and *Dryptosaurus* (0.4930) (e.g., Peacock et al., 2014). Furthermore, the undeformed proximal end of metatarsal IV has a much smaller width dorsoventrally and mediolaterally than *Appalachiosaurus montgomeriensis*, 48 mm to 83 mm and 30 mm to 82.6 mm, respectively (Table 1; Carr, Williamson & Schwimmer, 2005). The metatarsal II of YPM VPPU.021795, though eroded at the proximal end, is also much thinner proximally than the corresponding element in *Appalachiosaurus*, 80 to 100.9 mm dorsoventrally and 55 to 79.5 mm mediolaterally, respectively (Table 1; Carr, Williamson & Schwimmer, 2005). Among individuals of *Albertosaurus* and *Tyrannosaurus*, however, the proportions of metatarsals IV of comparable length are similar (e.g., Currie, 1998; Larson, 2008). Additionally, the AMNH *Albertosaurus* ~~metatarsi~~metatarsals do not differ in the proximal morphology of their metatarsals II and distal morphology of their metatarsals IV as between YPM VPPU.021795 and *Appalachiosaurus* (e.g., Currie, 1998). Therefore, the differences between the similarly

proximodistally long metatarsals of *Appalachiosaurus montgomeriensis* and YPM VPPU.021795 are indicative that the latter is distinct from the former. Differences between YPM VPPU.021795, *Dryptosaurus*, and *Appalachiosaurus* are listed in Table 2.

Biogeographical Considerations.

These comparisons (e.g., Table 2) suggest YPM VPPU.021795 represents a distinct taxon of tyrannosauroid on Appalachia. Notably, *Dryptosaurus* and *Appalachiosaurus* have been reported in other Campanian deposits of this landmass (e.g., Baird & Horner, 1979; Gallagher, 1993; Carr, Williamson & Schwimmer, 2005; Brusatte, Benson & Norell, 2011; Ebersole & King, 2011). However, the identification of a new taxon of tyrannosauroid from the Merchantville Formation hints at the possibility that Campanian bones assigned to the two named Appalachian tyrannosauroids could belong to other taxa. For example, teeth and a proximal manual phalanx collected from the Campanian Ellisdale fossil site were referred to as “cf. *Dryptosaurus*” by Gallagher (1993) and “*Dryptosaurus* sp.” by Grandstaff et al. (1992), while a tooth from the Campanian of Delaware was also compared to *Dryptosaurus* (Gallagher, 1993). More recently, Denton et al. (2011) assigned the teeth and limb bone fragment apparently referenced by Gallagher (1993) and Gallagher (1997) to indeterminate tyrannosauroids, along with several theropod phalanges. The author agrees with this assignment in light of the recognition of a distinct taxon of tyrannosauroid in the Atlantic Coastal Plain. Notably, several partial femora that compare favorably to that of *D. aquilunguis* have been collected from Campanian deposits in North Carolina (Baird & Horner, 1979; Weishampel & Young, 1996). Thus, it may be concluded that two to three tyrannosauroid taxa were present on Appalachia during the Campanian: that represented by YPM VPPU.021795, *Appalachiosaurus*

montgomeriensis, and *Dryptosaurus aquilunguis*/cf. *D. sp.*

In the western United States, nine or ten possible species [of Late Cretaceous tyrannosaurs](#) are known, ranging from the Prince Creek Formation of Alaska's north slope to a taxon from the El Gallo Formation of Mexico (e.g., Lambe, 1917; Holtz, 2004; Weishampel et al., 2004; Loewen et al., 2013; Thomson, Irmis & Loewen, 2013; Fiorillo & Tykoski, 2014; Peacock et al., 2014; Carr et al., 2017). This range is obviously larger latitudinally, as the main Late Cretaceous outcrop from Appalachia ranges only from New Jersey to the southern states of Alabama, Mississippi, and Georgia and westward to southeastern Missouri (e.g., Schwimmer, 1997; Schwimmer, 2002; Fix & Darrough, 2004). Thus, the number of tyrannosauroid taxa from Appalachia is not directly comparable to that from Laramidia, especially when the significant taphonomic biases against the preservation of dinosaurs from Appalachia are considered (e.g., Schwimmer, 1997; Schwimmer, 2002). There are presently six named tyrannosauroid species from the Campanian of the western United States (excluding Alaska) (*Bistahieversor sealeyi*, *Daspletosaurus torosus*, *Daspletosaurus horneri*, *Gorgosaurus libratus*, *Lythronax argestes*, *Teratophoneus curriei*)(e.g., Lambe, 1917; Russell, 1970; Weishampel et al., 2004; Carr & Williamson, 2010; Carr et al., 2011; Loewen et al., 2013; Carr et al., 2017), though Thomson, Irmis & Loewen (2013) and Peacock et al. (2014) described hindlimb elements of possibly distinct Campanian Laramidian tyrannosaurid taxa. Though the diversity of the clade on these two landmasses is hardly comparable at this date, the author would not be surprised if future review of Campanian Appalachian tyrannosauroid material yields higher diversity for the clade on the eastern landmass.

Finally, the results of the phylogenetic analysis of Tyrannosauroida including YPM VPPU.021795 and the morphology of the bones suggest the Merchantville taxon was an “intermediate” tyrannosauroid, supporting the hypothesis that Appalachian dinosaur faunas contained relict forms (e.g., Schwimmer, 1997). Brusatte, Benson & Norell (2011) discussed the possibility of a distinct eastern clade of Late Cretaceous tyrannosauroids. Though the assignment of YPM VPPU.021795 to another one of what Brusatte, Benson & Norell (2011) termed “intermediate” tyrannosauroid taxa provides further support that such forms were somewhat diverse on Appalachia, the phylogenetic analysis herein did not place *Dryptosaurus*, *Appalachiosaurus*, and the Merchantville taxon in a distinct clade (Supplementary Fig.1-2).

Conclusions.

A tyrannosauroid metatarsus from the Campanian Merchantville Formation of the Atlantic Coastal Plain can be reasonably distinguished from the two named Appalachian tyrannosauroid taxa (*Appalachiosaurus montgomeriensis* and *Dryptosaurus aquilunguis*), thus representing a potentially distinct taxon of tyrannosauroid in the Campanian of eastern North America. The specimen increases the known diversity of Appalachian tyrannosauroids and in addition The specimen also supports the previously stated hypothesis that Appalachian dinosaur faunas included relict forms that had survived on the landmass.

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