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

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For almost the entirely 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. Unfortunately, this latter landmass recorded only a sparse fossil record of dinosaurs, obscuring those forms which must have occupied the eastern portion of North America during this time. Appalachian dinosaur faunas, though obscure, do seem to be different in composition from Laramidian ones. One particular element of Appalachian faunas that has attracted significant attention are the non-tyrannosaurid tyrannosauroids of the continent. Tyrannosauroids on Appalachia, though represented by at least two taxa (*Appalachiosaurus montgomeriensis* and *Dryptosaurus aquilunguis*), as well as many partial and fragmentary skeletons and elements, are nevertheless poorly know when compared to their western contemporaries. Here, one specimen, the partial metatarsus of a tyrannosauroid from the Campanian Merchantville Formation of New Jersey, is described in detail. The specimen may be differentiated from *Appalachiosaurus montgomeriensis*, *Dryptosaurus aquilunguis*, and an unnamed specimen from the Maastrichtian of New Jersey by several notable morphological features outside the spectrum of individual variation, as well as by factoring in biogeographical considerations. The new specimen thus has significance for representing a new morphotype of tyrannosauroid from Appalachia, suggesting greater diversity of the clade on the landmass. Because of this, tyrannosaur diversity in the Campanian of Appalachia was compared to the diversity of tyrannosaurs in Laramidia during the same period to analyze the similarities and differences between the biogeography of tyrannosaurs on each landmass. The results suggest that Appalachian non-tyrannosaurid tyrannosauroids experienced a similar amount of diversity to tyrannosaurids in Laramidia during the Campanian.

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Abstract.

For almost the entirely 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. Unfortunately, this latter landmass recorded only a sparse fossil record of dinosaurs, obscuring those forms which must have occupied the eastern portion of North America during this time. Appalachian dinosaur faunas, though obscure, do seem to be different in composition from Laramidian ones. One particular element of Appalachian faunas that has attracted significant attention are the non-tyrannosaurid tyrannosauroids of the continent. Tyrannosauroids on Appalachia, though represented by at least two taxa (*Appalachiosaurus montgomeriensis* and *Dryptosaurus aquilunguis*), as well as many partial and fragmentary skeletons and elements, are nevertheless poorly know when compared to their western contemporaries. Here, one specimen, the partial metatarsus of a tyrannosauroid from the Campanian Merchantville Formation of New Jersey, is described in detail. The specimen may be differentiated from *Appalachiosaurus motngomeriensis*, *Dryptosaurus aquilunguis*, and an unnamed specimen from the Maastrichtian of New Jersey by several notable morphological features outside the spectrum of individual variation, as well as by factoring in biogeographical considerations. The new specimen thus has significance for representing a new morphotype of tyrannosauroid from Appalachia, suggesting greater diversity of the clade on the landmass. Because of this, tyrannosaur diversity in the

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Introduction.

The eastern portion of North America was separated from the American west during the Late Cretaceous by the Western Interior Seaway, forming a landmass known as Appalachia (e.g., Schwimmer, 2002). This eastern landmass is very poorly known in comparison to the western portion of North America (Laramidia), with dinosaurs only represented by isolated elements, fragmentary, and occasionally partial skeletons (e.g., Gallagher, 1993; Schwimmer, 1997; Ebersole & King, 2011).

Nevertheless, the dinosaur faunas of Appalachia have come to light, 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 repeatedly been found outside Tyrannosauridae in phylogenetic analyses (e.g., Carr, Williamson & Schwimmer, 2005; Brusatte, Benson & Norell, 2011; Loewen et al., 2013; Fiorillo & Tykoski, 2014). Unfortunately, the two holotype specimens of the two aforementioned taxa, a couple of fragmentary and undescribed partial specimens, and singular elements are all that is known from these eastern tyrant dinosaurs.

Here, the partial metatarsus of a tyrannosauroid is described, assignable to Tyrannosauroidea based on the morphology of the proximal articular surfaces of metatarsals II and IV indicating a metatarsal III that was was restricted to the plantar surface of the proximal end of the metatarsus, an autopomorphy of the group (Holtz, 2004). The specimen YPM-PU 21795, can been distinguished from *Appalachiosaurus montgomeriensis* (Carr, Williamson & Schwimmer, 2005), *Dryptosaurus aquilunguis* (e.g., Brusatte, Benson & Norell, 2011), and an unnamed specimen from the Maastrichtian of New Jersey housed in the American Museum of Natural History by a variety of morphological features. The specimen described herein thus represents a new morphotype and possibly unnamed taxon of tyrannosauroid dinosaur from Appalachia. Thus, the specimen adds to the diversity of the clade Tyrannosauroidea in the Campanian of eastern North America, suggesting multiple species of tyrannosauroid inhabited the Atlantic Coastal Plain and at least three species inhabited the east of Appalachia during the aforementioned stage of the Late Cretaceous.

Methods.

Permits.

No permits were required for the described 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” is used to refer to the collections of the American Museum of Natural History in New York, NY, the term “YPM-PU” is used to refer to the vertebrate paleontology collections of the Yale Peabody Museum in New Haven, CT, and the term “MCWSC RMM” is used to refer to the collections of the McWane Science Center in Birmingham, AL.

Photography.

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

Results.

Geological Setting.

The specimen described herein, YPM-PU 21795, was retrieved by Ralph Johnson and Ray Meyer of the Monmouth Amateur Paleontologist’s Society from an outcrop of the Merchantville Formation exposed along a portion of the southern bank of the Chesapeake & Delaware Canal approximately 0.75 miles east of Summite Bridge (Route 301) and 0.5 miles north of Summit, Delaware, at low tide. Gallagher (1993) described the Merchantville Formation as consisting of black to dark greenish-gray micaceous, silty clay to fine sand. Gallagher (1993) also noted the Merchantville Formation was early Campanian in age. Miller et al. (2004) found the Merchantville Formation to be latest Santonian to early Campanian in age, seated within the Merchantville Sequence, and to be consisting of glauconite sands and glauconitic clays. In addition to *Dryptosaurus aquilunguis* (this paper), tetrapods known from the Merchantville Formation include crocodylians, mosasaurs, turtles, the dinosaur *Hadrosaurus foulkii*, a specimen comparable to *Dryptosaurus*, and indeterminate ornithomimosaurs and hadrosaurs (Gallagher, 1993; Weishampel & Young, 1996).

Systematic Paleontology.

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

Theropoda Marsh (1881) sensu Gauthier (1986)

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

Tyrannosauroidea Walker (1964) sensu Holtz (2004)

Tyrannosauroidea indet.

Material: YPM-PU 21795, partial metatarsals II and IV of a tyrannosauroid dinosaur.

Description: YPM-PU 21795 (figure 1A-F; figure 2A-F) is the partial right metatarsus of a tyrannosauroid dinosaur, assignable to Tyrannosauroidea based on the morphology of the proximal articular surfaces of metatarsals II and IV showing the proximal surface of metatarsal III was crescent-shaped and limited to the plantar half of the proximal end of the metatarsus and that the specimen represents an arctometatarsalian tyrannosaur (Holtz, 2004). Notably, metatarsal II is incorrectly labeled as metatarsal IV and metatarsal IV is incorrectly labeled as metatarsal II in the Yale Peabody collections.

The right metatarsal II (figure 1A-F) has been noticeably eroded, though the dorsal surface is smooth and partially intact. The medial surface bears two slight ridges that extend downward from the proximal articular surface of metatarsal II with metatarsal III, forming a buttressing surface. In proximal view, the expanded proximal end has a morphology which differs from the corresponding surface in the right metatarsal II of *Appalachiosaurus montgomeriensis* in that in *A. montgomeriensis*, a more prominent articular facet for metatarsal

III exists (figure 19F in Carr, Williamson & Schwimmer, 2005). The medial condyle in YPM-PU 21795 is thus not as distinct as in *Appalachiosaurus*. Nevertheless, the articular surface for metatarsal III is still present in medial view and, along with the articulations present on the medial surface of metatarsal II, an arctometatarsalian condition for this tyrannosaur. Additionally, in YPM-PU 21795, a slight fossa separates the medial condyle from the ventral portion of the proximal surface. The partial shaft and proximal end of metatarsal II measure 310 mm long as measured along the lateral side, 80 mm wide dorsoventrally as measured along the proximal surface, and 55 mm wide mediolaterally as measured along the proximal surface.

The partial right metatarsal IV (figure 2A-F) is the better preserved of the two metatarsals. Towards the bottom of its dorsal surface, the specimen preserves scrapes consistent with evidence of shark scavenging (figure 2C) found in other specimens of dinosaur from the Atlantic Coastal Plain (e.g., Schein & Poole, 2014). This evidence of feeding activity by sharks confirms that the specimen floated out to sea before being deposited and preserved. The lateral surface is smooth, with a sharp ventral edge. The dorsal surface is smooth and rounded, expanding outward towards the proximal end of the specimen. The ventral surface mirrors the dorsal surface in the expansion. The medial surface is very flattened at the shaft, except for a ridge that extends diagonally from the ventral edge of the medial surface just above the diaphysis to the dorsal edge of the medial surface at the distal end of the shaft. This forms a teardrop-shaped buttressing surface for the articulation with metatarsal III. 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 suggests the presence of the autopomorphy of Tyrannosauroidea of having a proximally crescentic metatarsal III that is limited to the plantar half of the proximal face of the metatarsus (Holtz, 2004). This morphology, though found in the unnamed specimen from the Maastrichtian of New Jersey, is also much less pronounced in the just aforementioned specimen than in YPM-PU 21795 (pers. obs.), distinguishing the two specimens. Additionally, the unnamed New Jersey specimen's metatarsal IV has a much thinner shaft than that of YPM-PU 21795 (pers. obs.). The metatarsal IV of YPM-PU 21795 notably lacks the autopomorphic feature found in *Dryptosaurus aquilunguis* of having a shaft that in proximal view has a semioviod cross-section that is significantly mediolaterally wider than it is wide dorsoventrally (Brusatte, Benson & Norell, 2011). Thus, it cannot be assigned to *D. aquilunguis* and thus may be differentiated from that taxon. YPM-PU 21795 can further be distinguished from *Dryptosaurus* in that the proximal end is not as rectangular in the former as in the latter (figure 22E in Brusatte, Benson & Norell, 2011). The distal end of metatarsal IV was also preserved, though it was separated from the main portion of this metatarsal. The distal end, though badly worn and fragmented, still preserves important morphological features that distinguish YPM-PU 21795 from *Appalachiosaurus montgomeriensis* and *Dryptosaurus aquilunguis*. In distal view (figure 2F), the specimen is notably different in morphology from the corresponding element in the holotype of *Appalachiosaurus montgomeriensis* or *Dryptosaurus aquilunguis* (figure 19G in Carr, Williamson & Schwimmer, 2005; figure 22F in Brusatte, Benson & Norell, 2011). Unlike the condition in *A. montgomeriensis*, the distal end of metatarsal IV is rectangular rather than triangular in shape and has an even less noticeable sulcus separating the distal hemicondyles. 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. The portion of metatarsal IV that includes the partial shaft and proximal end measures 312 mm long along the lateral surface, 30 mm wide mediolaterally at the proximal surface, and 48 mm wide dorsoventrally at the proximal surface. The distal portion is 75 mm long as measured on its lateral surface, 36 mm wide dorsoventrally as measured at the distal surface, and 27 mm wide mediolaterally as measured along the distal surface.

Discussion.

Several morphologies found along the metatarsals II and IV of the specimen YPM-PU 21795 distinguish it from the taxa *Appalachiosaurus montgomeriensis* and *Dryptosaurus aquilunguis*, as well as differentiate it from an unnamed specimen from the Maastrichtian of New Jersey (AMNH 2550-2553). YPM-PU 21795 is also temporally differentiated from the latter specimen, and biogeographically so from known occurrences of *A. montgomeriensis*, which only have been reported to occur as far north as South Carolina (e.g., Carr, Williamson & Schwimmer, 2005; Ebersole & King, 2011; Schwimmer et al., 2015). In addition, YPM-PU 21795 corresponds to a much larger individual than AMNH 2550-2553 (pers. obs.). This size difference, however, may be due to ontogenic differences between the two specimens.

The morphological differences between YPM-PU 21795 and the holotype of *Dryptosaurus aquilunguis* are clearly beyond the point of intraspecific variation, as the former lacks an autopomorphy of the latter species when the same element from both specimens are compared. The morphological differences between *A. montgomeriensis* and YPM-PU 21795 are also significant and numerous enough to warrant the exclusion of the null hypothesis of YPM-

PU 21795 showing intraspecific variation within this species. The metatarsals are also less robust than those of most tyrannosaurid dinosaurs (e.g., Holtz, 2004). Additionally, as only non-tyrannosaurid tyrannosauroid dinosaur taxa are known from Appalachia (e.g., Carr, Williamson & Schwimmer, 2005; Brusatte, Benson & Norell, 2011; Loewen et al., 2013; Fiorillo & Tykoski, 2014), the assignment of YPM-PU 21795 to Tyrannosauroidea indet. is considered best.

Biogeographical Considerations.

From these morphological comparisons, it is clear that YPM-PU 21795 represents a distinct Campanian morphotype, and thus indeterminate taxon, of tyrannosauroid dinosaur from the Atlantic Coastal Plain of Appalachia. The identification of this likely new indeterminate taxon of tyrannosauroid from the Campanian of New Jersey increases the diversity of tyrannosauroids present on Appalachia during the Campanian to three species, as *Dryptosaurus* and *Appalachiosaurus* have been reported from other Campanian deposits corresponding to this landmass (e.g., Baird & Horner, 1979; Gallagher, 1993; Carr, Williamson & Schwimmer, 2005; Brusatte, Benson & Norell, 2011; Ebersole & King, 2011). Additionally, the specimen reveals the presence of at least two tyrannosauroid taxa in the Atlantic Coastal Plain during the Campanian, that represented by YPM-PU 21795 and *Dryptosaurus* (e.g., Gallagher, 1993; Weishampel & Young, 1996).

In the western United States, nine or ten possible species are known from Laramidia, ranging from the Prince Creek Formation of Alaska's north slope to a possibly unnamed animal from the El Gallo Formation of Mexico (e.g., Weishampel et al., 2004; Loewen et al., 2013; Thomson, Irmis & Loewen, 2013; Fiorillo & Tykoski, 2014). 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 (e.g., Schwimmer, 1997). Thus, the number of tyrannosaur taxa from Appalachia is not directly comparable to that from Laramidia, especially when the significant taphonomic biases against the preservation of dinosaurs from Appalachia is considered (e.g., Schwimmer, 1997; Schwimmer, 2002). Nevertheless, the five distinct tyrannosaurids from the western United States (in the lower 48) are comparable in number to the now three distinct tyrannosauroids from Appalachia (this paper), especially when again taphonomic biases against Appalachian dinosaurs are taken into account. Thus, it may be concluded that the tyrannosauroids of Appalachia probably enjoyed similar diversity across the landmass to tyrannosaurid dinosaurs on Laramidia.

Brief remarks on the biogeography of tyrannosauroids within the Atlantic Coastal Plain.

With the presence of two tyrannosauroid dinosaurs, *Dryptosaurus* and the morphotype represented by the Merchantville metatarsus, in the Campanian of the Atlantic Coastal Plain, a more detailed look into the biogeography of the Tyrannosauroidea in this area is warranted. During the Maastrichtian, *Dryptosaurus aquilunguis* is known from several units (including the New Egypt, Navesink, and Mt. Laurel Formations) in the Atlantic Coastal Plain (e.g., Gallagher, 1993; Weishampel & Young, 1996). Additionally, an unnamed specimen from the Maastrichtian Mt. Laurel or Navesink Formations of New Jersey (Gallagher, 1993), AMNH 2550-2553, shows differences with *Dryptosaurus* (pers. obs.) and may represent a new species. A description of this specimen is currently being written by the author. Thus, it may be that in both the Campanian and Maastrichtian, two tyrannosauroid genera coexisted in the Atlantic Coastal Plain.

In the western United States, *Gorgosaurus* and *Daspletosaurus* are both known from the Dinosaur Park Formation (e.g., Weishampel et al., 2004). The question then arises as to why only one taxon, *Appalachiosaurus montgomeriensis*, is present in the Campanian of the Gulf Coastal Plain (e.g., Weishampel et al., 2004; Ebersole & King, 2011). Possible competition for prey between tyrannosauroids and the massive crocodylian *Deinosuchus rugosus* has been discussed (e.g., Schwimmer, 2002), and such competition is one possible explanation for the lack of tyrannosauroid dinosaurs in the southeastern United States where *Deinosuchus* was extremely common (e.g., Schwimmer, 2002). However, *Deinosuchus* is importantly present in the Campanian Marshalltown Formation of New Jersey (where evidence of predation by the crocodylian on dinosaurs has been found)(e.g., Schwimmer, 2002). Additionally, the presence of the same number of possibly distinct tyrannosauroids in the Atlantic Coastal Plain in the Campanian *and* Maastrichtian (before and after the disappearance of *Deinosuchus* from eastern North America)(e.g., Schwimmer, 2002) suggests other environmental factors may have played a role in determining the diversity of tyrannosauroids locally in Appalachia. This latter hypothesis is further supported by the presence of both *Appalachiosaurus* and *Dryptosaurus* in the Carolinas (e.g., Baird & Horner, 1979; Schwimmer et al., 2015). Such and understanding of local dinosaur biogeography on Appalachia thus must wait for the collection of more specimens from across eastern North America.

Conclusions.

A tyrannosauroid metatarsus from the Campanian Merchantville Formation of the Atlantic Coastal Plain can be distinguished from the two named Appalachian tyrannosauroid taxa (*Appalachiosaurus montgomeriensis* and *Dryptosaurus aquilunguis*) and a possibly distinct specimen from the Maastrichtian of New Jersey, thus representing a new morphotype and possibly distinct taxon of tyrannosauroid in the Late Cretaceous of eastern North America. The specimen increases the diversity of Appalachian tyrannosauroids, causing the number of distinct western tyrannosaurids and eastern tyrannosauroids from the lower 48 to be comparable. Locally, the Merchantville metatarsus evinces the presence of two distinct morphotypes of tyrannosaur in the Atlantic Coastal Plain. Nevertheless, the question of why only one species of tyrannosauroid (*Appalachiosaurus montgomeriensis*) existed in the Gulf Coastal Plain during the Campanian (unlike the situation in the Atlantic Coastal Plain or Carolinas) remains unsolved.

Acknowledgements.

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Figure 1(on next page)

Metatarsal II of the Merchantville Tyrannosauroid Specimen YPM-PU 21795.

Metatarsal II in lateral (A), medial (B), dorsal (C), ventral (D), and proximal (E) views. Scale bar = 100mm.

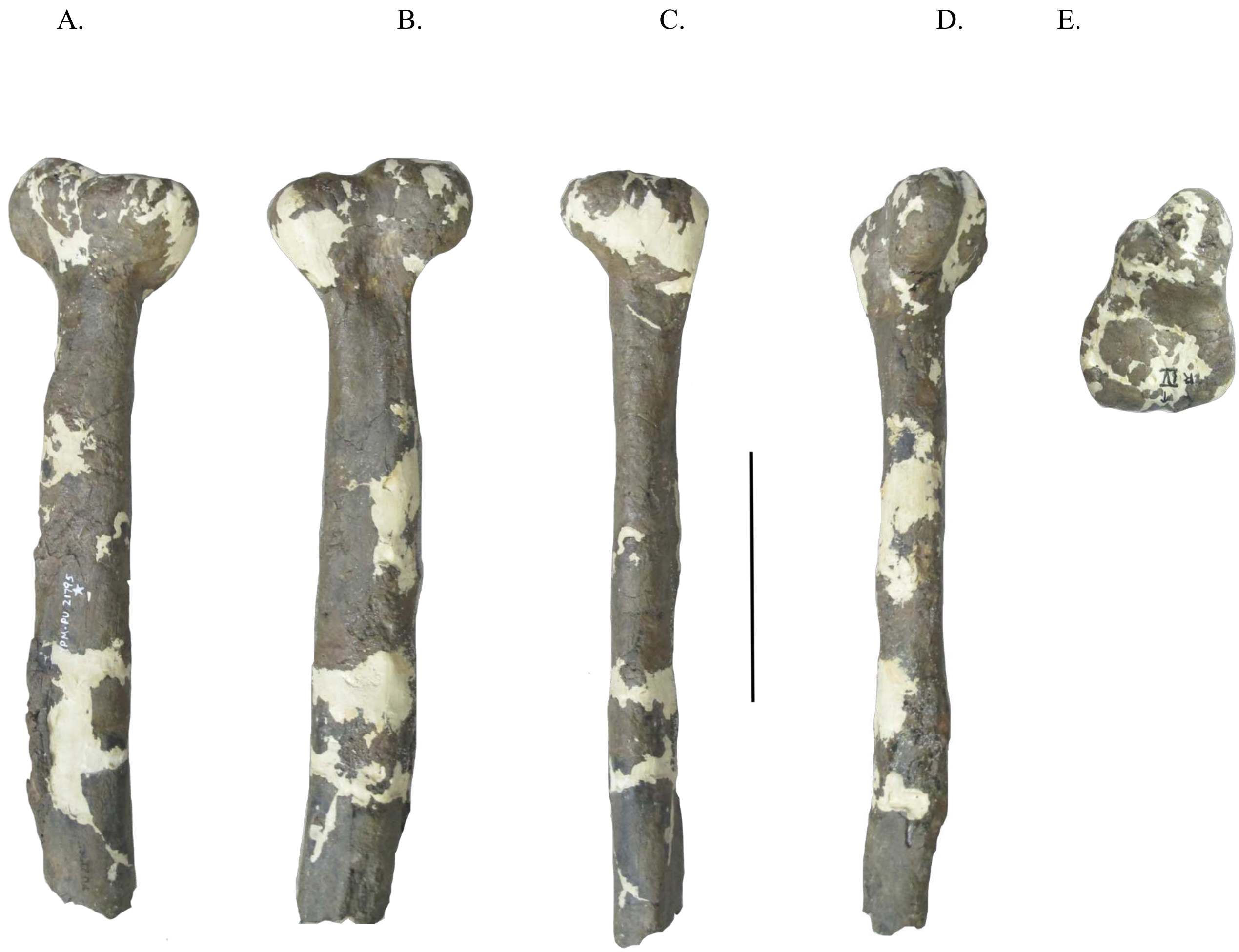
A.
B.
C.
D.
E.

Figure 2(on next page)

Metatarsal IV of the Merchantville Tyrannosauroid Specimen YPM-PU 21795.

Metatarsal IV in lateral (A), medial (B), dorsal (C), ventral (D), proximal (E), and distal (F) views. Scale bar = 100mm.

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