

## **Theropod specimens from the Navesink Formation and their implications for the Diversity and Biogeography of Ornithomimosaur and Tyrannosauroids on Appalachia**

The sparse dinosaur record of eastern North America has rendered the dinosaurs of the Late Cretaceous landmass of Appalachia obscure. This landmass, isolated from the western landmass Laramidia by a great inland sea known as the Western Interior Seaway, may have been a safe haven for dinosaur species which would be replaced on Appalachia's western contemporary. An excellent example of these isolated forms are the tyrannosaurs of Appalachia, which have not only been grouped outside Tyrannosauridae proper in phylogenetic analyses, but also bear distinct morphologies, including a gigantic manus in one form, from these 'western tyrants'. However, Appalachian tyrannosaurs are only represented currently by the two valid taxa *Dryptosaurus aquilunguis* and *Appalachiosaurus montgomeriensis*, both which are only known from partial skeletons with few overlapping elements. Recently, the generic name *Teihivinator* was given to another tyrannosaur named "*Laelaps*" *macropus* by Cope (1868) by Yun (2017). However, examination of the specimens by the author show morphologies at odds with the morphological descriptions given by Yun (2017). The tyrannosaur named by Yun (2017), known from partial lower hindlimb elements including the portions of two metatarsals and a partial tibia, is shown herein to be a chimaera of ornithomimosaur and tyrannosauroid hindlimb elements. The several different dinosaur specimens which compose the syntypes of "*Teihivinator*" include three ornithomimosaur pedal phalanges with affinities to derived ornithomimid taxa, a proximal end of the right metatarsal II and a distal end of the right metatarsal II from either ornithomimosaur or tyrannosauroids, and a partial tibia of a tyrannosauroid distinct from *Dryptosaurus* or *Appalachiosaurus* but nevertheless considered here to be from an indeterminate taxon based on the lack of observable autapomorphies and issues with the comparability of the specimen to other taxa. The

specimens are nevertheless important for revealing further the theropod fauna of the Maastrichtian Navesink Formation of New Jersey, as well as for possibly increasing the diversity of tyrannosauroids and further illuminating the presence of ornithomimosaur on Appalachia.

1 Theropod specimens from the Navesink Formation and their implications for the Diversity and  
2 Biogeography of Ornithomimosaur and Tyrannosauroids on Appalachia

3  
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5  
6 Abstract.

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8 Late Cretaceous landmass of Appalachia obscure. This landmass, isolated from the western  
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19 with the morphological descriptions given by Yun (2017). The tyrannosaur named by Yun  
20 (2017), known from partial lower hindlimb elements including the portions of two metatarsals  
21 and a partial tibia, is shown herein to be a chimaera of ornithomimosaur and tyrannosauroid  
22 hindlimb elements. The several different dinosaur specimens which compose the syntypes of

23 “*Teihivenator*” include three ornithomimosaur pedal phalanges with affinities to derived  
24 ornithomimid taxa, a proximal end of the right metatarsal II and a distal end of the right  
25 metatarsal II from either ornithomimosaur or tyrannosauroids, and a partial tibia of a  
26 tyrannosauroid distinct from *Dryptosaurus* or *Appalachiosaurus* but nevertheless considered  
27 here to be from an indeterminate taxon based on the lack of observable autapomorphies and  
28 issues with the comparability of the specimen to other taxa. The specimens are nevertheless  
29 important for revealing further the theropod fauna of the Maastrichtian Navesink Formation of  
30 New Jersey, as well as for possibly increasing the diversity of tyrannosauroids and further  
31 illuminating the presence of ornithomimosaur on Appalachia.

### 32 Introduction.

34 The Late Cretaceous saw a major period of change in the geography and ecology of  
35 North American ecosystems. During the Cenomanian Stage of the Late Cretaceous, the Western  
36 Interior Seaway separated the terrestrial ecosystems of the eastern portion of North America with  
37 those of the American west, in turn affecting the faunas of both the east and west of the continent  
38 by subjecting each to isolation for millions of years. While in the west, it is known that the  
39 ancestors of the iconic *Tyrannosaurus rex* evolved reduced forelimbs and massive, powerful  
40 skulls, the tyrannosaurs of the eastern portion of North America, at that time a landmass called  
41 Appalachia (e.g., Sampson et al., 2010; Loewen et al., 2013), have remained more obscure, and  
42 rarely are associated or partial skeletons ever found. The two most complete tyrannosaurs from  
43 Late Cretaceous continent described so far are *Dryptosaurus aquilunguis* and *Appalachiosaurus*  
44 *montgomeriensis*, originally known from the Maastrichtian New Egypt Formation of New Jersey

45 and from the middle Campanian Demopolis Chalk Formation of Alabama, respectively (e.g.,  
46 Cope, 1866; Marsh, 1877; Weishampel et al., 2004; Carr, Williamson & Schwimmer, 2005;  
47 Weishampel, 2006; Brusatte, Benson & Norell, 2011). Additional remains assigned to  
48 *Dryptosaurus* have been recovered from the Marshalltown Formation-bearing Ellisdale  
49 microfossil site, the Mt. Laurel Formation at upper Hop Brook, and the Navesink Formation at  
50 Big Brook in New Jersey (Krause & Baird, 1979; Baird & Galton, 1981; Gallagher & Parris,  
51 1986; Grandstaff et al., 1992). Possible additional remains of this taxon have been reported from  
52 North Carolina (Baird & Horner, 1979). *Appalachiosaurus* is also known from multiple other  
53 Campanian units in the southeastern United States (e.g., Ebersole & King, 2011). Recently,  
54 Schwimmer et al. (2015) described teeth and bones of *Appalachiosaurus montgomeriensis* from  
55 eastern South Carolina. Remains from the Missouri Chronister Site have also been assigned to an  
56 undetermined genus of tyrannosaur (Fix & Darrough, 2004).

57 The holotype specimens of *D. aquilunguis* and *A. montgomeriensis* have been found as  
58 “intermediate” tyrannosauroid dinosaurs in multiple phylogenetic analysis, unlike the derived  
59 tyrannosaurids of the western portion of North America (e.g., Brusatte, Benson & Norell, 2011;  
60 Loewen et al., 2013; Fiorillo & Tykoski, 2014; Brusatte et al., 2016; Brusatte & Carr, 2016).  
61 Additionally, striking morphologies completely absent in western tyrannosaurs, such as the  
62 gigantic manus with large unguals present in *D. aquilunguis*, are known from Appalachian taxa.  
63 However, the lack of overlap of the skeletal elements of *Dryptosaurus aquilunguis* and  
64 *Appalachiosaurus montgomeriensis* has made their evolutionary relationships ambiguous  
65 (Brusatte, Benson & Norell, 2011).  
66

67 Very recently, a third tyrannosauroid, “*Teihivenator macropus*”, was described from the  
68 Maastrichtian Formation of New Jersey by Yun (2017). The author, who was also describing and  
69 reevaluating the specimens AMNH 2550-2553 at the time of the publication of Yun (2017),  
70 though he arrived at different conclusions regarding these specimens. Examination of the  
71 specimens by the author reveal that the syntypes of “*Teihivenator*” actually represent specimens  
72 of ornithomimosaur and indeterminate tyrannosauroids. One of these specimens, a partial  
73 eroded tibia, is from a tyrannosauroid that may be distinguished from *Dryptosaurus aquilunguis*  
74 and *Appalachiosaurus montgomeriensis*, suggesting increased diversity for tyrannosauroids on  
75 Appalachia through the Maastrichtian. However, the eroded partial tibia is not diagnostic enough  
76 to support the existence of a distinct taxon and not comparable to several tyrannosaur specimens  
77 from distinct or likely distinct taxa, and thus “*Teihivenator macropus*” is considered a *nomen*  
78 *dubium*. Additionally, several of the specimens included in the syntypes of the aforementioned  
79 dubious taxon are assignable to ornithomimosaur and have morphological affinities to derived  
80 ornithomimids.

81 The reassignment of the syntypes of “*Teihivenator*” to multiple different species may be  
82 seen as another example of the mistaken association of dinosaur specimens leading to the naming  
83 of a new genus. Baird & Horner (1979), for example, reevaluated Edward Drinker Cope’s  
84 holotype specimen of *Hypsibema crassicauda*, finding it to include elements assignable to cf.  
85 *Dryptosaurus aquilunguis* and indeterminate hadrosaurids in addition to the lectotype specimen  
86 of *H. crassicauda*.

87  
88 Methods.

89 Permits.

90 No permits were required for the described study, which complied with all relevant regulations.

91 Access to the collections at the American Museum of Natural History was given by Carl

92 Mehling.

93  
94 Institutional Abbreviations.

95 The term “AMNH FARB” is used to refer to the fossil amphibian, reptile and bird collections of  
96 the American Museum of Natural History.

97  
98 The specimens described herein were photographed using a Canon Powershot G12 camera and  
99 cropped using Apple Preview.

100  
101 Results.

102 Geologic Setting. AMNH 2550-2553 have been thought as coming from the Maastrichtian Mt.  
103 Laurel, Navesink, or New Egypt Formations of New Jersey (e.g., Horner, 1979; Gallagher,  
104 1993). Several clues are of help when determining exactly from which of these formations these  
105 coelurosaurian elements were recovered. In his original description of the fossils, Leidy (1865)  
106 cites the location of the discovery of these fossils as in Monmouth County, New Jersey. Cope  
107 (1870) gives a brief description of the stratigraphy of the unit from which the specimens which  
108 constitute the holotype of this new tyrannosaur species were recovered, stating it was from the  
109 “Upper Cretaceous, upper green sand bed Monmouth Co., N. J.” Gallagher (1997) gives a more  
110 detailed location of discovery and discoverer of AMNH 2550-2553, the former being a marl pit

111 in Marlboro, New Jersey, and the later being the notable geologist George Cook. Most recently,  
112 Gallagher et al. (2014) identified the location of the discovery of AMNH 2550-2553 as the Big  
113 Brook site in Marlboro, New Jersey, noting the Navesink and Mt. Laurel Formations to both be  
114 present there. Yun (2017) also suggested a Navesink Formation origin for the specimens, which  
115 fits with the coloration of the syntypes. Indeed, AMNH 2550-2553 have coloration that  
116 resembles fossils found from the Navesink (e.g., Anné, Hedrick & Schein, 2016). Finally,  
117 Brusatte et al. (2012) agree that the origin of these specimens was the Navesink Formation.  
118 Notably, the Navesink Formation is a marine deposit.

119 Systematic Paleontology.

120 Dinosauria Owen 1842 sensu Padian and May 1993

121 Theropoda Marsh 1881 sensu Gauthier 1986

122 Coelurosauria Huene 1914 sensu Sereno et al. 2005

123 Tyrannosauroida Walker 1964 sensu Holtz 2004

124 Tyrannosauroida indet.

125 Specimen: AMNH 2550, proximal and distal ends of a right tibia.

126 The proximal end of the right tibia of a tyrannosauroid dinosaur (figure 1.A-F) is eroded, likely  
127 from water wear. The specimen measures 95 mm proximodistally and 94 mm dorsoventrally as  
128 measured on the lateral surface, 72 mm mediolaterally and 93 mm proximodistally as measured  
129 dorsally, 93 mm dorsoventrally and 89 mm proximodistally as measured on the medial surface,  
130 and 35 mm mediolaterally and 45 mm proximodistally on the ventral surface. The proximal  
131 surface is 95 mm mediolaterally and 60 mm dorsoventrally. The cnemial crest has been partially  
132 destroyed by erosion, and thus the autapomorphy of the cnemial crest being visible in ventral



133 view of proximal tibia given by Yun (2017) for “*Teihivenator*” cannot be supported. The lateral  
134 portion of the proximal articular surface and lateral portion of the shaft are also not preserved.  
135 The incisura tibialis is subtle as in *Dryptosaurus aquilunguis* (Brusatte et al., 2011), and the  
136 presence of an anterior process cannot be determined. The medial posterior condyle is well-  
137 preserved and triangular. The side of the medial posterior condyle facing the lateral posterior  
138 condyle is eroded, and the lateral posterior condyle is also too poorly preserved for  
139 morphological description, thus undermining one other autopomorphy listed by Yun (2017) for  
140 “*Teihivenator*”. This is the position of the medial condyle being higher than that of the lateral  
141 condyle. The lateral surface of the tibia is much more strongly curved towards the proximal  
142 surface than in *Dryptosaurus aquilunguis*. The preserved portion of the lateral posterior condyle  
143 and the medial posterior condyle are separated by a deep, I-shaped notch, noted as an  
144 autopomorphy of “*Teihivenator*” by Yun (2017). This notch is deeper than in *Dryptosaurus* or  
145 *Appalachiosaurus* (Carr, Williamson & Schwimmer, 2005; Brusatte, Benson and Norell, 2011),  
146 though is very similar in shape to that of the tibia of *Appalachiosaurus* (Carr, Williamson &  
147 Schwimmer, 2005). Considering the eroded nature of the specimen, the understanding of this  
148 notch as a distinguishing feature of the tyrannosaur to which this tibia corresponds is considered  
149 ambiguous. The protuberance within this notch suggested as an autopomorphy of “*Teihivenator*”  
150 by Yun (2017) is considered herein to be a taphonomic relic from erosion that simply represents  
151 a non-eroded portion of the surface of the posterior lateral condyle. The rounded medial edge of  
152 the medial posterior condyle resembles the condition in other tyrannosauroids (Holtz, 2004). As  
153 in *Dryptosaurus aquilunguis*, there is a notable depression in the center of the proximal articular  
154 surface of the tibia (Brusatte et al., 2011). The medial posterior condyle is strongly offset from

155 where the cnemial crest is indicated to have been located. The proximal and distal ends of the  
156 shaft of the tibia indicate an elongate tibia was present in this tyrannosauroid, a feature that is  
157 indicative of placement in Tyrannosauroidea (Holtz, 2004).

158 The distal end of the right tibia (figure 1.A-F) is well-preserved. The distal end is  
159 dorsoventrally flattened. The lateral malleolus reaches its end very slightly distal to the medial  
160 malleolus, though the lateral malleolus shows slight signs of wear. Nevertheless, the position of  
161 the lateral malleolus relative to the medial malleolus distinguishes this tibia from *Dryptosaurus*  
162 *aquilunguis* or *Appalachiosaurus montgomeriensis* (Carr, Williamson & Schwimmer, 2005;  
163 Brusatte, Benson & Norell, 2011). Nevertheless, the identification of this feature as an  
164 autapomorphic trait of the tibia by Yun (2017) is considered nebulous, as Yun (2017) even noted  
165 that other derived tyrannosauroids display this feature. The lateral malleolus extends 20 mm  
166 outward laterally (=33% of the adjacent shaft). Though the medial malleolus does not protrude as  
167 strongly outward in this tyrannosaur as in *Dryptosaurus*, in the case of *Dryptosaurus* this  
168 morphology of the distal end of the tibia was because of erosional damage (Brusatte, Benson &  
169 Norell, 2011). Muscle scars may also be preserved on the distal end of the tibia. As in  
170 *Dryptosaurus*, the specimen shows the distal margin of the tibia was concave (Brusatte, Benson  
171 & Norell, 2011). The articular facet faces anteriorly as in other tyrannosaurs (Holtz, 2004). The  
172 dorsal surface 143 mm proximodistally, 90 mm mediolaterally at the malleoli (55 mm at the  
173 shaft), 140 mm proximodistally and 95 mm mediolaterally (55 mm at the shaft) at the ventral  
174 surface, 140 mm dorsoventrally and 32 mm proximodistally at the lateral surface, and finally 95  
175 mm mediolaterally, and 37 mm and 23 mm dorsoventrally at the lateral and medial malleoli,  
176 respectively, as measured on the distal surface. This tibia belongs to a small tyrannosauroid of

177 around 5 to 6 meters in length (based on comparisons with *Appalachiosaurus*)(Carr, Williamson  
178 & Schwimmer, 2005).

179 Dinosauria Owen 1842 sensu Padian and May 1993

180 Theropoda Marsh 1881 sensu Gauthier 1986

181 Coelurosauria Huene 1914 sensu Sereno et al. 2005

182 Tyrannosauroida (Walker 1964 sensu Holtz 2004) or Ornithomimosauria (Barsbold 1976 sensu  
183 Choiniere, Forster & de Klerk 2012)

184 Tyrannosauroida indet. or Ornithomimosauria indet.

185 Specimens: AMNH 2553, proximal end of right metatarsal II or IV.

186 Description: The proximal end of metatarsal IV or II (figure 2.A-E) is notably different in

187 coloration and preservation from the partial tibia, suggesting the specimens were not associated.

188 The coloration of the bone shaft not destroyed by pyrite disease is a dark black, whereas the tibia

189 ranges in color from brownish-grey to dark grey in color. Though Yun (2017) identified this

190 element as the proximal end of metatarsal II, the specimen may also be half of the proximal end

191 of metatarsal IV of a tyrannosauroid dinosaur. This is due to the fact that, as Yun (2017) noted, a

192 portion of the specimen is missing. Though the specimen (though more gracile) indeed resembles

193 the metatarsal II of *Appalachiosaurus montgomeriensis*, an unnamed specimen of tyrannosauroid

194 from the Merchantville Formation, and other tyrannosauroids (e.g., Holtz, 2004; Carr,

195 Williamson & Schwimmer, 2005, pers. obs.), the morphology of the proximal surface may also

196 represent half of the characteristic v-shaped notch for the articulation of metatarsal III restricted

197 to the plantar half of the foot that is found in derived tyrannosauroids (e.g., Holtz, 2004). In

198 either case, the specimen represents a metatarsal more gracile than either metatarsals II and IV of

199 *Appalachiosaurus* and tyrannosaurids (e.g., Holtz, 2004). As Yun (2017) noted, *Dryptosaurus*  
200 *aquilunguis* has a relatively gracile metatarsal IV, and so an affinity with *Dryptosaurus* is  
201 certainly worth considering for this specimen. However, the incomplete nature of this metatarsal  
202 IV does not allow for the identification of the possible autapomorphy on this specimen that was  
203 identified on the metatarsal IV of *D. aquilunguis* found by Brusatte, Benson & Norell, (2011).  
204 Brusatte et al. (2012) assigned this specimen to a derived taxon of ornithomimid from the  
205 Navasink Formation based on what they interpreted as a weakly-developed articular surface for  
206 metatarsal III.

207 The lateral face of the proximal end of AMNH 2553 measures 139 mm proximodistally  
208 and 34 mm dorsoventrally at its proximal end, whilst the same measurements of the medial side  
209 are 139 mm and 43 mm, respectively. The dorsal face is also 139 mm proximodistally and is 5  
210 mm mediolaterally at its proximal end. The same two measurements for the ventral surface are  
211 139 mm and 23 mm.

212 Dinosauria Owen 1842 sensu Padian and May 1993

213 Theropoda Marsh 1881 sensu Gauthier 1986

214 Coelurosauria Huene 1914 sensu Sereno et al. 2005

215 Tyrannosauroida (Walker 1964 sensu Holtz 2004) or Ornithomimosauria (Barsbold 1976 sensu

216 Choiniere, Forster & De Klerk 2012)

217 Tyrannosauroida or Ornithomimosauria indet.

218 Specimen: AMNH 2552, distal end of metatarsal II.

219 Description: This gracile distal end of the metatarsal II of a coelurosaurian dinosaur (figure 3.A-

220 E) may be assignable either to Tyrannosauroida or Ornithomimosauria. This assignment is

221 based on the size of the specimen in conjunction with the articular surface for metatarsal III on  
222 the medial face of AMNH 2552 suggesting an arctometatarsalian or sub-arctometatarsalian  
223 condition where the metatarsals are closely appressed. The size of the specimen and the unfused  
224 nature of the metatarsus suggests against assignment of AMNH 2552 to an australian. Additionally,  
225 the specimen is more robust than the metatarsals of troodontids (e.g., Makovicky & Norell,  
226 2004). Like AMNH 2553, the erosional patterns and color of AMNH 2552 suggest against  
227 association with AMNH 2550. Notably, the coloration and wear patterns on AMNH 2552 closely  
228 resemble those of AMNH 2553, suggesting possible association between the two specimens.

229 The lateral face of this metatarsal II measures 100 mm proximodistally and 22 mm  
230 dorsoventrally at the condyles, whereas the medial face is 101 mm proximodistally and 35 mm  
231 dorsoventrally at the condyles. The dorsal surface also measures 101 mm proximodistally, while  
232 mediolaterally it measures 31 mm at the distal end. The ventral surface is 100 mm  
233 proximodistally and 40 mm mediolaterally at the distal end. The distal surface is 38 mm wide  
234 dorsoventrally and 37.8 mm wide mediolaterally.

235 Dinosauria Owen 1842 sensu Padian and May 1993

236 Theropoda Marsh 1881 sensu Gauthier 1986

237 Coelurosauria Huene 1914 sensu Sereno et al. 2005

238 Ornithomimosauria Barsbold 1976 sensu Choiniere, Forster & de Klerk 2012

239 Ornithomimosauria indet.

240 Specimen: AMNH 2551, three pedal phalanges.

241 Description: The three pedal phalanges included in the syntypes of "*Teihivenator*" *macropus* are  
242 identified herein as the left and right pedal phalanges III-1 and the right pedal phalanx II-1 of an

243 indeterminate ornithomimosaur or possibly ornithomimid dinosaur. Yun (2017) noted the  
244 distinguishability of these phalanges from those of other tyrannosaurs based on the presence of  
245 proximally oriented process extending from the proximal ends of each specimen, also noting that  
246 these specimens (along with the rest of the syntypes of “*Teihivinator macropus*”) were referred  
247 to ornithomimosaur in multiple studies. However, no comparison of these phalanges with those  
248 of ornithomimosaur was made in Yun (2017). The dorsoventrally straightened nature of the  
249 left and right pedal phalanges III-1 is clearly more congruent with that of the corresponding  
250 phalanges of ornithomimosaur than the robust, curved pedal phalanges of derived  
251 tyrannosauroids (e.g., Holtz, 2004; Makovicky, Kobayashi & Currie, 2004). Examination of  
252 these phalanges reveals that the processes are rather the ventral lateral and medial edges of the  
253 proximal articular facets of each phalanx, forming tips proximally but also appearing on the  
254 ventral surface towards the diaphysis of the phalanges as ridges that intersect to form a triangular  
255 shape in ventral view. In fact, the specimens are almost identical to the corresponding elements  
256 in the pes of *Struthiomimus altus* (Osborn, 1921), where these process-like tips of bone at the  
257 ventrolateral and ventromedial ends of the rim surrounding the proximal articular facet of the  
258 phalanges are clearly visible. This morphology of phalanx appears in many different genera of  
259 ornithomimosaur, including possibly in the basalmost ornithomimosaur taxon *Nqwebasaurus*  
260 *thwazi* (figure 14.B in Choiniere, Forster & de Klerk, 2012). Additional figures of  
261 ornithomimosaur pedal specimens showing this morphology may be found in Cullen et al.  
262 (2013). Yun (2017) also noted the presence of this morphology in other clades of theropod  
263 dinosaur. As such, these specimens cannot in good faith be used to justify the presence of a  
264 distinct taxon of tyrannosauroid or even assigned to Tyrannosauroidea. These phalanges are grey

265 in color and almost match the color of the tyrannosauroid tibia described above, though they are  
266 clearly more well-preserved. Thus, these phalanges likely hail from the Navesink Formation,  
267 where a distinct taxon of ornithomimid of possibly similar phylogenetic derivation to  
268 ornithomimid taxa like *Gallimimus* and *Ornithomimus* known for now as “*Ornithomimus*”  
269 *antiquus* is also found (Brusatte et al., 2012). The morphological similarity of these phalanges  
270 with *Struthiomimus altus* especially supports their origin from a derived ornithomimosaur. The  
271 presence of such an animal in Appalachia would be intriguing, considering the basal position of  
272 the tyrannosauroids, hadrosaurids, and hadrosauroids of Appalachia when compared to related  
273 genera from other parts of the globe (e.g., Schwimmer, 1997; Carr, Williamson & Schwimmer,  
274 2005; Brusatte, Benson & Norell, 2011; Prieto-Marquez, Erickson & Ebersole, 2016).

275 The left pedal phalanx III-1 measures 80 mm proximodistally, 50 mm mediolaterally at  
276 the proximal articular facet, and 29 mm mediolaterally at the distal end. The medial surface  
277 measures 82 mm proximodistally, 40 mm dorsoventrally at the proximal end and 22 mm at the  
278 condyles. The ventral surface measures 80 mm proximodistally, 35 mm mediolaterally at the  
279 proximal end, and 26 mm at the condyles. The lateral surface is 83 mm long proximodistally, and  
280 dorsoventrally measures 35 mm at the proximal end and 22 mm at the condyles. The distal end is  
281 20 mm dorsoventrally between the condyles and 35 mm mediolaterally. The proximal end is 35  
282 mm dorsoventrally and 5 mm mediolaterally.

283 The dorsal face of the right pedal phalanx II-1 is 90 mm proximodistally, 40 mm  
284 mediolaterally at the proximal end and 30 mm at the distal, whereas the ventral face in the same  
285 dimensions is 89 mm, 29 mm, and 26 mm. The medial surface is 93 mm proximodistally, 47 mm  
286 dorsoventrally at the proximal end and 31 mm at the distal end. The lateral face is 91 mm

287 proximodistally, 50 mm mediolaterally at the proximal end, and 25 mm at the distal end. The  
288 proximal surface is 39 mm dorsoventrally and 36 mm mediolaterally, whereas the distal surface  
289 is 25 mm in both the same two dimensions.

#### 291 Discussion.

292 The syntypes of “*Teihivenator macropus*” are herein shown to be the bones of both  
293 indeterminate tyrannosauroids and ornithomimosaur. Additionally, the autopomorphies on the  
294 tibia of “*Teihivenator macropus*” listed by Yun (2017) are unable to be found on the specimen  
295 AMNH 2550 or are found in other tyrannosauroids. Thus, the syntypes of “*Teihivenator*  
296 *macropus*” are a chimaera and the tibia lacks any non-dubious autopomorphies. As such,  
297 “*Teihivenator macropus*” must be regarded as a *nomen dubium*. Nevertheless, the proximal and  
298 distal ends of the Navesink tibia assignable to a tyrannosauroid are distinct enough from  
299 *Appalachiosaurus* and *Dryptosaurus* to suggest the presence of another morphotype and possibly  
300 distinct taxon of tyrannosauroid in New Jersey during the Maastrichtian. Notably, the small size  
301 of the tibia when compared to those of the aforementioned Appalachian tyrannosauroid taxa  
302 (suggesting an animal ~5-6 meters in length) may indicate that the tibia was from an immature  
303 specimen of tyrannosaur. Additionally, the tibia is unfortunately not comparable to the  
304 tyrannosauroid morphotype represented by a partial metatarsus from the Merchantville  
305 Formation of New Jersey (pers. obs.). As such, AMNH 2550 is likely best thought of as the tibia  
306 of an indeterminate tyrannosauroid that may represent a distinct but indeterminate taxon of  
307 tyrannosaur on Appalachia. In addition to this possibly distinct taxon of tyrannosauroid, the  
308 Navesink Formation has also been documented as including *Dryptosaurus aquilunguis*,



309 *Hadrosaurus* “*cavatus*”, “*Ornithomimus*” *antiquus*, and an indeterminate theropod based on a  
310 tooth known as “*Diplotomodon horrificus*” (e.g., Gallagher, 1993; Gallagher, 1997; Weishampel  
311 & Young, 1996; Weishampel, 2006). The presence of two genera of tyrannosauroids in this unit  
312 allies it in faunal composition with the Merchantville Formation of New Jersey (fauna includes  
313 *Dryptosaurus* sp. and an indeterminate but distinct Merchantville tyrannosauroid)(Gallagher,  
314 1993; pers. obs.) and the the temporally equivalent and geographically adjacent faunas of the Tar  
315 Heel and Coachman Formations (fauna includes *Dryptosaurus aquilunguis* and  
316 *Appalachiosaurus montgomeriensis*)(e.g., Baird & Horner, 1979; Weishampel & Young, 1996;  
317 Schwimmer et al., 2015). The presence of two tyrannosauroids in the same ecosystem is also  
318 known in a few units from Laramidia (e.g., Weishampel et al., 2004).

319 The ornithomimosaur or tyrannosauroid metatarsals described herein may be assignable  
320 to either group. Further study of these elements and comparison with the metatarsals of both  
321 ornithomimosaur and tyrannosauroids is needed before more definite assignments may be made.

322 Finally, the phalanges included in AMNH 2551 suggest the presence of a derived taxon  
323 of ornithomimosaur in the Navesink Formation, supporting the hypothesis of Brusatte et al.  
324 (2012). Whether these pedal elements are assignable to “*Ornithomimus*” *antiquus* will require the  
325 collection of further ornithomimosaur specimens from the Maastrichtian of the Atlantic Coastal  
326 Plain.

327 The assignment of the remains of several clades of dinosaur to a single taxon is not an  
328 occurrence unique to the case of “*Teihivenator macropus*” in eastern dinosaur paleontology. As  
329 noted, Baird & Horner (1979) revised the assignment by Cope (1869) of tyrannosauroid and  
330 indeterminate hadrosaurid material to the holotype of the gigantic hadrosaurid *Hypsibema*

331 *crassicauda* based on the close location of the specimens. Thus, the cases of both *Hypsibema*  
332 *crassicauda* and “*Teihivenator macropus*” represent cautionary tales of mis-assignment from  
333 appeared association of specimens.

#### 334 Conclusions.

335 The syntypes of “*Teihivenator macropus*” represent a chimaera composed of the tibia of an  
336 indeterminate though possibly distinct tyrannosauroid, metatarsals possibly assignable to either  
337 tyrannosauroids or ornithomimosaur, and pedal phalanges likely assignable to a derived  
338 ornithomimosaur. The specimens increase the current understanding of theropod dinosaurs from  
339 the Navesink Formation, and have implications for the biogeography and diversity of  
340 ornithomimosaur and tyrannosauroids on the landmass of Appalachia.

341 Additionally, the case of “*Teihivenator macropus*” should be considered a cautionary tale  
342 of dinosaur paleontology, showing that possible association of partial disarticulated specimens  
343 (especially from marine deposits) should be rigorously scrutinized before the specimens are  
344 remarked to have come from a single animal.

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Figure 1. Tibia of an indeterminate taxon of tyrannosauroid, AMNH 2550. Tibia in lateral (A), medial (B), dorsal (C), ventral (D), proximal (E), and distal (D) views. Scale bar = 50 mm.

A.



B.



C.



D.



E.



F.



Figure 2. Metatarsal II or IV of an ornithomimosaur or tyrannosauroid dinosaur, AMNH 2553.

Metatarsal in lateral (A), medial (B), dorsal (C), ventral (D), and proximal (E) views. Scale bar = 50 mm.

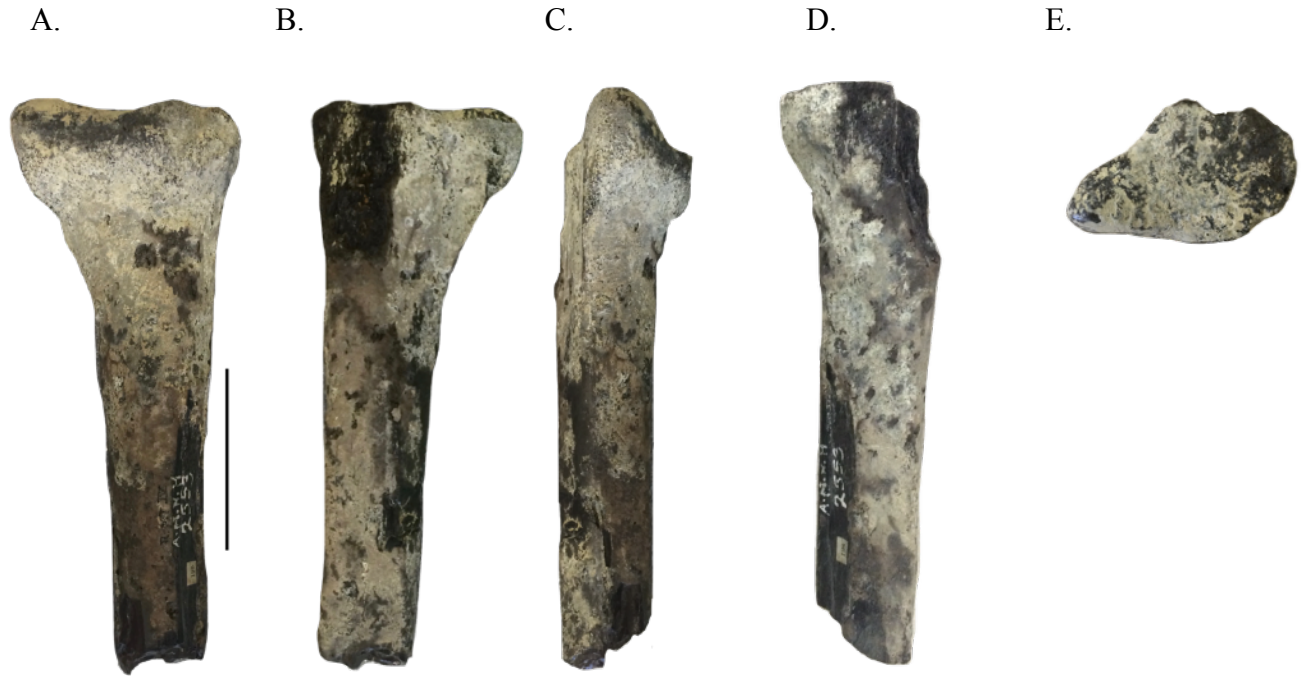


Figure 3. Distal metatarsal II of a tyrannosauroid or ornithomimosaur, AMNH 2552. Metatarsal in lateral (A), medial (B), dorsal (C), ventral (D), and distal (E) views. Scale bar = 50 mm.

A.



B.



C.



D.



E.





Figure 4. Phalanges of a derived ornithomimosaur, AMNH 2551. Phalanges in medial (A) dorsal (B), and ventral (C) views. Scale bar = 50 mm.

A.



B.



C.

