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Theropod hindlimbs with feeding and other traces reveal ecosystem dynamics in the Maastrichtian of eastern North America

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Maastrichtian of eastern North America

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Abstract.

Direct documentation of the ecology of past life is often rare when the fossil record is comparatively poor, as in the case of the terrestrial fauna of the Maastrichtian of eastern North America. Here, I describe a femur and partial tibia shaft assignable to theropods from the Maastrichtian Big Brook locality of New Jersey. The former, identifiable to a previously undetected morphotype of large ornithomimosaur, bears several scrapes identifiable as the feeding traces of sharks, adding to the collection of terrestrial vertebrate remains bearing such marks from the state. The latter is littered with tooth marks and punctures from possibly multiple crocodyliform individuals, the first documented occurrence of such traces on dinosaur bone from the Maastrichtian of the Atlantic Coastal Plain. Additionally, its surface is dotted with likely traces of invertebrates, revealing a microcosm of biological interaction from the Maastrichtian New Jersey shoreline. Previously, the massive Campanian crocodylian taxon *Deinosuchus rugosus* and the slightly smaller Cenomanian-age Texas crocodyliform *Deltasuchus motherali* have been shown as important drivers of terrestrial vertebrate taphonomy in eastern North America. The report of crocodyliform bite marks on the ornithomimosaur metatarsal shaft in this manuscript reveals that crocodylians continued to play role in the taphonomy of large dinosaurs in eastern North America through the end of the Mesozoic. The preserved invertebrate traces add to the sparse record of their traces on dinosaur bone, and the presence of shark scrapes on the femur supports the “bloat-and-float” model of terrestrial vertebrate fossil deposition in eastern North America.

Introduction.

Despite the hindrance of a poor fossil record, one pattern that has emerged in the study of the ecology and taphonomy of eastern North America is the frequency of vertebrate remains — especially those of turtles and dinosaurs— that bear bite marks or are corroded from digestion by crocodylians. Such marks have been documented in fossils from the Cenomanian Woodbine Formation of Texas and referred to the taxon *Deltasuchus motherali* (Main, Noto & Drumheller, 2012; Noto, Main & Drumheller, 2012; Main, 2013; Adams et al., 2017). In the Campanian, evidence of crocodyliform feeding on dinosaurs from multiple Campanian geological units of the southeastern United States and from the Campanian Marshalltown Formation of New Jersey have been attributed to the massive crocodylian *Deinosuchus rugosus*, which may have been extremely common on the eastern North America coastline (e.g., Schwimmer et al., 1993; Gallagher, 1995; Schwimmer, 1997, 2002, 2010; Schwimmer et al., 2015). However, no record of large crocodyliform bite marks on dinosaur material has been reported from the Maastrichtian of eastern North America, when *Deinosuchus* disappears from the fossil record (Schwimmer, 2002).

In the Maastrichtian of the Atlantic Coastal Plain, crocodyliforms are represented by various forms slightly to considerably smaller than *D. rugosus*, including *Borealosuchus threeensis*, *Thoracosaurus neocesariensis*, *Hyposaurus rogersii*, and *Elosuchus minor* (De Kay, 1842; Carpenter, 1983; Parris, 1986; Gallagher, 1993; Brochu, 2006; Brochu et al., 2012). Among these, *Borealosuchus threeensis* and *Thoracosaurus neocesariensis* seem to have grown the largest, with specimens from the Maastrichtian of the Atlantic Coastal Plain assignable to these taxa achieving sizes of 5 or more meters, perhaps 7 to 8 in one specimen of the latter (e.g., Schwimmer, 2002; Brochu et al., 2012).

Unlike crocodyliform bite marks, traces on dinosaur bones from sharks have been recovered from the Campanian and Maastrichtian of eastern North America. Such finds include the heavily shark-bitten partial femur of a diminutive adult hadrosaurid from the Hornerstown Formation (Schein and Poole, 2014) and other remains of hadrosaurids, nodosaurids, and tyrannosauroids (e.g., Carpenter et al., 1995; Schwimmer, 1997; Schwimmer, Stewart & Williams, 1997; Everhart & Ewell, 2006; Brownstein, 2017). Some of these occurrences of shark feeding traces on dinosaur bones may be caused by individuals of the medium-sized species *Cretolamna appendiculata*, and there is direct evidence (embedded teeth) to show that *Squalicorax kaupi* occasionally scavenged dinosaur bone (e.g., Schwimmer, 1997; Schwimmer et al., 1997; Schein & Poole, 2014). These shark feeding traces on dinosaur bones have been noted in the study of eastern North American dinosaur taphonomy to support the prevalence of the “bloat and float” hypothesis in eastern North American dinosaur preservation, whereby dinosaur carcasses washed out to sea, remained buoyant in the water due to an internal buildup of gas, and slowly lost body parts that would become fossilized on the sea floor (Schwimmer, 1997).

Invertebrate traces on dinosaur bones are somewhat uncommon, though insect burrows on such specimens have been extensively described in the literature (e.g., Rogers, 1992; Hasiotis et al., 1999; Paik, 2000; West & Martin, 2002; Hasiotis, 2004; Kirkland & Bader, 2007; Roberts, Rogers & Foreman, 2007; West & Hasiotis, 2007; Bader, Hasiotis & Martin, 2009; Xing et al., 2015). Traces on dinosaur bone vary greatly in morphology, with marks assigned to invertebrates including pits, striations, tunnels, and scratches (e.g., Bader, Hasiotis & Martin, 2009; Xing et al., 2015). These marks have been shown to be important indicators of the taphonomy of the bones on which they lie (e.g., Martin & West, 1995; Hasiotis et al., 1999; West & Hasiotis, 2007;

Bader, Hasiotis & Martin, 2009). In the Maastrichtian of the Atlantic Coastal Plain, invertebrate borings are common on the fossil shells of the bivalves *Exogyra costata* and *Pycnodonte mutabilis* and are attributed to the sponge *Cliona cretacica* (e.g., Fenton & Fenton, 1932).

In the 1970s, two partial theropod hindlimb bones were recovered from the heavily collected Big Brook fauna by Gerard R. Case and Ralph O. Johnson. One consists of the partial shaft of a tibia, the other the partial distal end of a femur. The femur is assignable to an as-yet-unrecognized morphotype of large ornithomimosaur of similar size to the Asian taxon *Gallimimus* and an unnamed animal from the Campanian Dinosaur Park Formation of Alberta (e.g., Longrich, 2008). Both New Jersey specimens show marks attributable to feeding, the tibia shaft bearing ones from crocodyliforms and the femur from sharks, and function as important insights into the paleoecology of the Maastrichtian terrestrial community of the east coast of North America (Fiorillo, 1991; Gallagher, 1995; Schwimmer, 1997; Chure et al., 1998; Schwimmer, 2002; Rogers et al., 2003; Jennings & Hasiotis, 2006; Reisz & Tsuji, 2006; Schwimmer, 2010; Noto, Main & Drumheller, 2012; Main, 2013).

Materials & Methods.

Permits.

No permits were needed for this study, which abided by all relevant rules and regulations.

Access to the collections of the Peabody Museum of Natural History was provided by Daniel Brinkman.

Identification and documentation of traces.

The surfaces of both bones were extensively searched for fossil traces. Artifacts of preparation were carefully identified and excluded. The presence of any preparation artifacts potentially interpretable as trace fossils is unlikely, as both YPM VPPU.021825 and YPM VPPU.022361

were collected from the surface after being eroded out of Cretaceous exposures on the banks of Big and Hop brooks. Probable traces were reviewed, photographed, and measured using digital calipers. The width of each trace was taken along each's midway, with length measured along each's greatest axis. Described traces were compared with previously documented traces on modern and fossilized bones, as in previous studies (e.g., Noto, Main & Drumheller, 2012; Boyd et al., 2013).

The nomenclature of Njau and Gilbert (2016) was followed for the discussion of crocodyliform feeding traces, which were identified based on their criteria and through comparisons with other descriptions of fossil crocodyliform feeding traces in the literature. Shark feeding traces were identified based on morphologies presented for such traces in previously published studies, as were those of invertebrates.

Geological Setting.

The tibia shaft portion YPM VPPU.021825 was recovered from Maastrichtian deposits at the Big Brook site of Monmouth County, New Jersey. There has been some debate as to the exact provenance of the majority of fossils collected from this waterway after being eroded from the sediments of the riverbanks (e.g., Lauginger, 1986; Becker & Chamberlain, 2000; Gallagher et al., 2014), but recent studies have found that most specimens of Late Cretaceous dinosaurs from the site are from the early to mid-Maastrichtian Navesink Formation (e.g., Miller et al., 2004; Brusatte et al., 2012). The partial distal femur YMP VPPU.022361 was recovered from the Navesink Formation at Hop Brook near Homdel, New Jersey (Baird, 1986).

The environment represented by the Navesink Formation (69-67 Ma; Miller et al., 2004) at Big Brook is marine in origin, representing a transgression of the Atlantic Ocean (e.g., Gallagher et al., 1986; Lauginger, 1986; Gallagher, 1993; Weishampel & Young, 1996; Miller et

al., 2004; Parris, Grandstaff & Gallagher, 2004). The Navesink Formation at Big Brook represents the deepest, most saline environment at the locality and is heavily fossiliferous at some intervals (Gallagher et al., 1986). Terrestrial vertebrate fossils from the site include the worn bones of lambeosaurines and indeterminate hadrosaurids, nodosaurids, tyrannosauroids, and ornithomimosaurids representing the dinosaur fauna (e.g., Gallagher et al., 1986; Gallagher, 1993; Weishampel & Young, 1996; Brusatte et al., 2012). The marine vertebrate fauna is extensive, including the marine crocodyliform *Thoracosaurus*, several different species of marine turtles and mosasaurs, and a menagerie of Chondrichthyes and Osteichthyes taxa (e.g., Gallagher et al., 1986; Lauginger, 1986; Gallagher, 1993).

Systematic paleontology.

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

Theropoda Marsh (1881) sensu Gauthier (1986)

Theropoda indet.

Material: YPM VPPU.021825, partial tibia shaft.

Referral: The tibia may be attributed to a theropod based on its hollow interior.

Description YPM VPPU.021825 (Fig. 1A-E) is the partial tibia shaft of a large theropod (e.g., Baird, 1986; Gallagher, 1993). The bone still preserves a poorly developed articular surface for the fibula on its medial surface that is bordered by two slight, proximodistally running ridges.

The bone is straightened and, in cross-sectional view, has a greater dorsoventral than mediolateral width. Measurements of this specimen may be found in Table 1.

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

Theropoda Marsh (1881) sensu Gauthier (1986)

Coelurosauria von Huene (1914) sensu Sereno, McAllister & Brusatte (2005)

160 Ornithomimosauria Barsbold 1976 sensu Choiniere, Forster & De Klerk (2012)

161 Ornithomimosauria indet.

162 Material: YPM VPPU.022361, partial distal left femur.

163 Referral: The femur may be tentatively assigned to Ornithomimosauria based on a combination

164 of morphological features, as it was too incomplete to be included in phylogenetic analyses. The

165 femur YPM VPPU.022361 is assigned to Ornithomimosauria based on its (1) elongate nature,

166 which was originally used by Baird (1986) for this assignment, (2) the presence of a thin crest

167 extending proximally from the distal medial condyle, and (3) heavily separated distal condyles

168 (e.g., Makovicky, Kobayashi & Currie, 2004). Besides ornithomimosaurids, only dromaeosaurids

169 and tyrannosauroids are known from the Campanian-Maastrichtian of Appalachia (e.g., Baird &

170 Horner, 1979; Gallagher, 1993; Weishampel & Young, 1996; Kiernan & Schwimmer, 2004; Carr

171 et al., 2005; Brusatte et al., 2011; Brusatte et al., 2012; Schwimmer et al., 2015; pers. obs.). All

172 described dromaeosaurids from Appalachia are smaller than the theropod to which the YPM

173 specimen described herein belongs (Kiernan and Schwimmer, 2004; Schwimmer et al., 2015;

174 pers. obs.), and dromaeosaurids of similar size to the dinosaur to which the Big Brook limb bone

175 belongs have more robustly built femora with only slightly separated distal condyles and lack a

176 distal medial ridge (e.g., Norell & Makovicky, 2004). The femur is also differentiated from

177 tyrannosauroids like *Dryptosaurus* and *Appalachiosaurus* based on the features noted above (fig.

178 16A-D in Carr et al., 2005; fig. 15 in Brusatte et al., 2011; pers. obs.).

179 Description: YPM VPPU.022361 (Fig. 2A-F) is the distal femur of a large ornithomimosaur. The

180 specimen is of comparable measurements to the femora of *Gallimimus* (Table 1; Osmólska,

181 Roniewicz & Barsbold, 1972; Baird, 1986) and is hollow. Portions of both the lateral and medial

182 distal femoral condyles are preserved, separated by a prominent intercondylar groove. On the

medial surface of the medial distal condyle, a ridge originates that extends proximodorsally. The femur is slightly divergent dorsally towards its distal end in medial and lateral views. Muscle attachment scars are present on the preserved portion of the lateral surface of the bone.

Remarks on vertebrate feeding traces on specimens.

Crocodyliforms: Four tooth marks identified as those of crocodyliforms are present on the lateral surface YPM VPPU.021825. The lateral surface of the bone preserves four crocodyliform feeding traces, including three that are adjacent to each other and may represent a single biting event (Fig. 1D). Of these three adjacent bite marks, the distal is the largest and most rounded, with the pits proximal to the largest pit curving towards the dorsal surface. This indicates that the marks were left by teeth of the premaxilla and distal maxilla or the front of the dentary of a biting crocodyliform. Distal to all these pits on the bone, a single ovoid pit is also present. All of these marks appear as jagged pits (Njau & Gilbert, 2016), and their measurements are catalogued in Table 2.

On the medial surface of YPM VPPU.021825, three definite and several possible pits are preserved (Fig. 2B, E). One large, rounded pit exhibits a shape consistent with other reports of crocodyliform bite marks on dinosaur remains (e.g., Schwimmer, 2002; Noto, Main & Drumheller, 2012; Boyd et al., 2013). This pit is proximally adjacent to the edge of a major area of spalled bone and laterally and dorsally to major breaks in the bone surface (Fig. 1B, E). A large, elongate, bisected pit sits within the distal portion of smaller area of spalled bone (Fig. 1B, E). These areas of bone spalling are consistent with periosteal/subcambial bone spalling seen from crocodyliform bites (e.g., Njau & Blumenschine, 2006, 2012; Drumheller, 2007, 2012; Njau & Gilbert, 2016). Several other rounded marks sit in the larger spalled bone region, though these may be from invertebrates (see below). Both spalled regions of bone are regarded as caused

by crocodyliform feeding due to the presence of pits on the borders of each. Along with those from the marks on the lateral surface, measurements of pits present on the medial surface are catalogued in Table 2.

Sharks: At least three gently arched scores are present on the distal ornithomimosaur femur YPM VPPU.023361 (Fig. 2C). None of these scores are paired and each clearly came from only one tooth cusp, none bear serration striations, and all are deepened, varying slightly in width at their midpoints. The scores are concentrated on the ventral surface of the distal femur YPM VPPU.023361, although several scrapes on the lateral and dorsal surfaces may also be shark feeding traces. Measurements of these marks may be found in Table 2.

Invertebrates: The medial surface of the partial tibia shaft YPM VPPU.021825 is littered with a variety of very shallow marks (Fig. 1B, E), varying in shape from thin, linear depressions to ovoid and circular ones. These marks are biological based on their rounded, nearly radially and bilaterally symmetrical outlines. These shapes are unlike those expected from artifacts of erosion, which would be comparatively jagged and appear as heavy abrasions, rather than small, detailed marks, on the bones. The majority of the marks on the surface of this bone appear as tubular grooves that are oriented sub-parallel to the longitudinal axis of the bone and do not extend past the cortical bone layer. Another morphotype of invertebrate trace appears as shallow, circular depressions that are present across the medial surface of the tibia shaft.

Discussion.

Assignment of traces on the described bones to specific clades.

The large, deepened pits and major patches of bone spalling on the theropod tibia YPM VPPU.021825 are identified as crocodyliform feeding traces based on several criteria. The possibilities that these feeding traces are those of theropod dinosaurs, mammals, plesiosaurs, or

mosasaurs, which are all represented in the Navesink (e.g., Gallagher, 1993), are rejected based on several lines of evidence. Firstly, these bite marks were clearly made by an organism that possessed unserrated, incrassate or conical teeth due to the lack of corresponding striations near or within any of the pits. Secondly, the deepened, extensive nature of the pits and spalled bone are consistent with the trace maker possessing a powerful bite. This first observation eliminates theropod dinosaurs, whose serrated teeth leave striations on bone (e.g., Fiorillo, 1991; Horner & Lessem, 1993; Erickson & Olson, 1996; Carpenter, 1998; Chure et al., 1998; Jacobsen, 2001; Hyslop & Boyd, 2004; Fowler & Sullivan, 2006; Longrich & Ryan, 2010; Noto, Main & Drumheller, 2012; de Valais et al., 2012; Xing et al., 2012; Boyd et al., 2013; Hone & Tanke, 2015), and the second further eliminates the Maastrichtian theropod dinosaurs present in the Atlantic Coastal Plain that were large enough to produce the marks on YPM VPPU.021825 (tyrannosauroids) had heavily ziphodont, serrated teeth and relatively lightly built skulls (Brusatte et al., 2011).

Mammals may also be eliminated as agents of the pits and spalling on YPM VPPU.021825. Firstly, the size of the animal that YPM VPPU.021825 represents is clearly much larger than non-avian dinosaurs that preserve evidence of mammalian feeding on their bones (e.g., Hu et al., 2005). Secondly, the bisected pit on the ventral surface of the tibia shaft is inconsistent with a mammalian feeding trace, but is so with one of a crocodyliform (e.g., Njau & Blumenschine, 2006; Boyd et al., 2013; Njau & Gilbert, 2016). These marks are also inconsistent with the shallow to deepened linear scores and gouges of mosasaur bite marks (e.g., Einarrson et al., 2010) or the shallow, linear scrapes of those of plesiosaurs (e.g., Martin, Rothschild & Burnham, 2016).

The pits and areas of spalled bone on YPM VPPU.021825 satisfy three of the five criteria of Njau & Blumensiche (2006) for the identification of crocodyliiform bite marks: the rarity of crocodyliiform bite marks in the assemblage (only the metatarsal described herein has been noted as possessing such pits out of the dozens of dinosaur specimens collected from Big Brook; Gallagher, 1993; pers. obs.), the presence of bisected pits, and the lack of evidence for gnawing on the bone. Additionally, the marks may satisfy the criterion of Njau & Blumensiche (2006) for crocodyliiform bite mark identification that the marks are populous on bones useful for leverage, though not enough are present on the preserved portion of the tibia to definitively state so. The fragmentary nature of YPM VPPU.021825 is interpreted as a taphonomic relic from erosion and deposition at sea rather than an indication of the type of organism that left the pits and spalling on its surface (e.g., Njau and Blumensiche, 2006; Boyd et al., 2013), as other theropod bones from the Atlantic Coastal Plain bearing feeding traces clearly attributable to large crocodyliiforms are also fragmentary limb shafts (e.g., Schwimmer, 2002, 2010).

Only one crocodyliiform from the Navesink Formation has been reported: *Thoracosaurus neocesariensis* (De Kay, 1842; Gallagher, 1993; Schwimmer, 2002). At least one specimen of this taxon is known that reached a length of ~7-8 meters (Schwimmer, 2002). However, the deepened pits and extensive bone spalling on the metatarsal YPM VPPU.021825 are inconsistent with the morphology of the conical, elongate, slightly hooked teeth of *Thoracosaurus* (e.g., Brochu, 2004). As the Navesink Formation represents the deepest marine environment out of the units present at Big Brook, the possibility that a previously undetected taxon of crocodyliiforms living inland or along the coast inflicted such marks is certainly possible. Whatever taxon or taxa of crocodyliiform were the makers of the pits and spalling areas on YPM VPPU.021825, they

possessed the ability to prey or scavenge on dinosaurs of more than 3 meters in length and inflict somewhat extensive damage to bones (Fig. 1).

Regarding the scores present on the femur, similar marks on dinosaur and other vertebrate bones deposited in marine settings have been attributed to sharks (e.g., Everhart et al., 1995; Schwimmer, 1997; Everhart, 1999; Shimada & Everhart, 2004; Shimada & Hooks, 2004; Everhart & Ewell, 2006; Schein & Poole, 2014). Though no teeth are imbedded in YPM VPPU.022361, the morphology of the scores is highly consistent with those on dinosaur bones with embedded shark teeth (e.g., Schwimmer, 1997), warranting their identification as shark feeding traces.

Gallagher (1993) reported two genera of shark in the Navesink Formation. Individuals of *Squalicorax pristodontus* may be eliminated as candidates for the bite marks on YPM VPPU.022361, as the teeth of that taxon were serrated and would have left striations on the femur (e.g., Schein and Poole, 2014). The goblin shark *Scapanorhynchus texanus*, a deep-water predator that possessed elongate, un-serrated teeth, is considered the more likely candidate for inflicting the scrapes on YPM VPPU.022361 among the two shark taxa reported from the Navesink Formation (Gallagher, 1993), though any confident assignment of these traces to a specific shark taxon is impossible.

The tubular invertebrate traces on YPM VPPU.021825 are somewhat comparable to the insect borings on dinosaur bones described by Bader, Hasiotis & Martin (2009) and Xing et al. (2015). Borings on a plesiosaur bone from New Jersey may be from an invertebrate similar to *Lithophaga* (Johnson, pers. commun. 2018), which is known to burrow into corals and stromatolites (e.g., Jones & Pemberton, 1988; Akpan, 1991). *Lithophaga ripleyana* is the species known from the Navesink Formation (e.g., Gallagher, Paris & Spamer, 1986). However,

Lithophaga leaves larger, deeper clavate borings than those on the tibia shaft. Shallow, circular marks on the tibia shaft are also interpreted as invertebrate traces. Both morphotypes of traces identified as those of invertebrates are nearly absent from the lateral surface of YPM VPPU.021825, indicating the medial surface was exposed to the water column and the lateral surface was buried in the substrate.

Taphonomy of the dinosaur bones.

The presence of the several different traces on the dinosaur specimens described herein is important in illuminating both the taphonomy of terrestrial vertebrate remains in the Maastrichtian marine deposits of the Atlantic Coastal Plain and the paleoecology of the near-shore environments of the region. The bite marks of mid-sized crocodyliforms (in comparison to the estimated sizes of other crocodyliforms to which bite marks have been assigned; e.g., Noto, Main & Drumheller, 2012; Boyd et al., 2013) on the partial tibia shaft YPM VPPU.021825 may suggest the specimen first underwent some taphonomic event in a near-shore environment before transport onto the sea floor. In Texas, an attritional vertebrate assemblage likely created by the large crocodyliform *Deltasuchus motherali* has been documented at the Arlington Archosaur site of the Cenomanian Woodbine Formation, which preserves a near-shore environment (e.g., Noto, Main & Drumheller, 2012; Adams et al., 2017). It is certainly possible that such an event occurred in the taphonomy of YPM VPPU.021825 before it was washed into the Atlantic Ocean. Once deposited at sea, the medial surface of YPM VPPU.021825 likely faced into the water column to experience significant abrasion on account of the invertebrates, before washing out to sea and experiencing significant disarticulation and erosion. The rounded state of the edges of YPM VPPU.021825 is consistent with the bone being deposited in the deep, marine environment represented by the Navesink Formation rather than being reworked from older deposits.

Furthermore, the lack of dinosaur remains from the exposures of earlier Campanian and latest Maastrichtian-Paleogene units exposed at Big Brook (e.g., Gallagher, 1993) suggests YPM VPPU.021825 originated in Campanian-Maastrichtian to Maastrichtian horizon.

The distal femur YPM VPPU.022361 seems to have undergone a longer period of erosion at sea based on its rough, exfoliated surface and the presence of shark feeding traces on the bone. Several features of YPM VPPU.022361 support the prevalence of the “bloat-and-float” model (e.g., Schwimmer, 1997) among Maastrichtian terrestrial vertebrate remains in the Atlantic Coastal Plain. These include (1) the identification of the bone as the distal portion of a limb bone, (2) the presence of shark feeding traces on the bone, and (3) the bone’s eroded, fragmentary state. These taphonomic artifacts are also consistent with the preservation of the bone in the deep marine setting of the Navesink Formation.

These bones thus support the presence of two taphonomic models among terrestrial vertebrate remains in the Navesink Formation. The first includes taphonomic events in near-shore environments, such as predation or scavenging by crocodyliforms and other carnivores, and later deposition and taphonomy from both biotic (possible worm and indeterminate invertebrate traces) and abiotic (water erosion) on the seafloor. The second is the “bloat-and-float” model of Schwimmer (1997) whereby dinosaur skeletons are washed out to sea and bones on the fringes of the skeleton fall to the sea floor and experience significant water wear, with scavenging by marine predators occurring throughout the process. Implications for the Maastrichtian vertebrate fauna of the Atlantic Coastal Plain.

In addition to their taphonomic significance, the dinosaur femur and crocodyliform traces on the tibia described herein also add to the current vertebrate fauna of the Navesink Formation a large morphotype of ornithomimosaur and a possibly new species of large crocodyliform. Large

ornithomimosaur have also been documented in the Campanian of Mongolia (representing two clades; e.g., Osmólska, Roniewicz & Barsbold, 1972; Lee et al., 2014) and Alberta and the Maastrichtian of the United States (“*Struthiomimus*” *sedens*; e.g., Longrich, 2008), and so their presence in the Maastrichtian of eastern North America is relatively unsurprising.

Conclusions.

Partial hindlimb bones of large ornithomimosaur from the Maastrichtian of New Jersey preserve several types of traces, including those assignable to sharks, previously undetected crocodyliforms, and invertebrates. These fossils have the potential to inform taphonomic models for vertebrate fossil deposition in the Atlantic Coastal Plain during that time, evincing the presence of two modes in the Navesink Formation environment. One included taphonomic stages in both near-shore and deep-sea settings, whereas the other was more exclusively marine. Additionally, the specimens add to the diversity of vertebrates in the Maastrichtian of eastern North America, suggesting the presence of large ornithomimosaur and a potentially new crocodyliform morphotype.

Institutional Abbreviations.

YPM VPPU, Princeton University collection in the Division of Paleontology, Yale Peabody Museum, New Haven, CT, United States.

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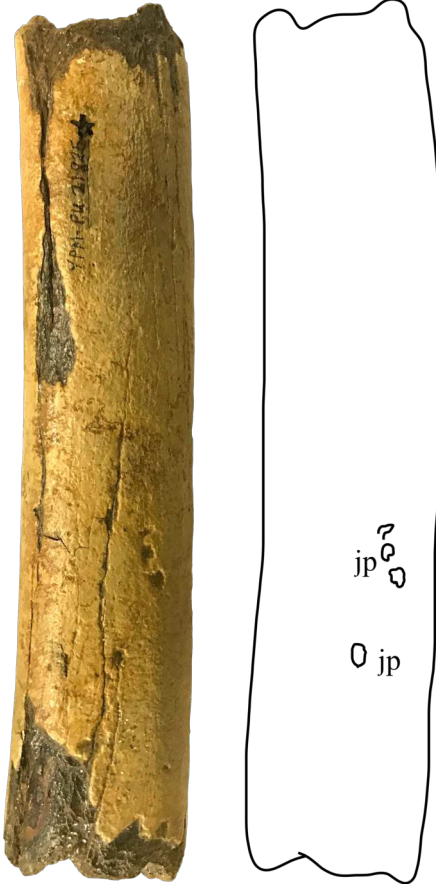
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Figure 1(on next page)

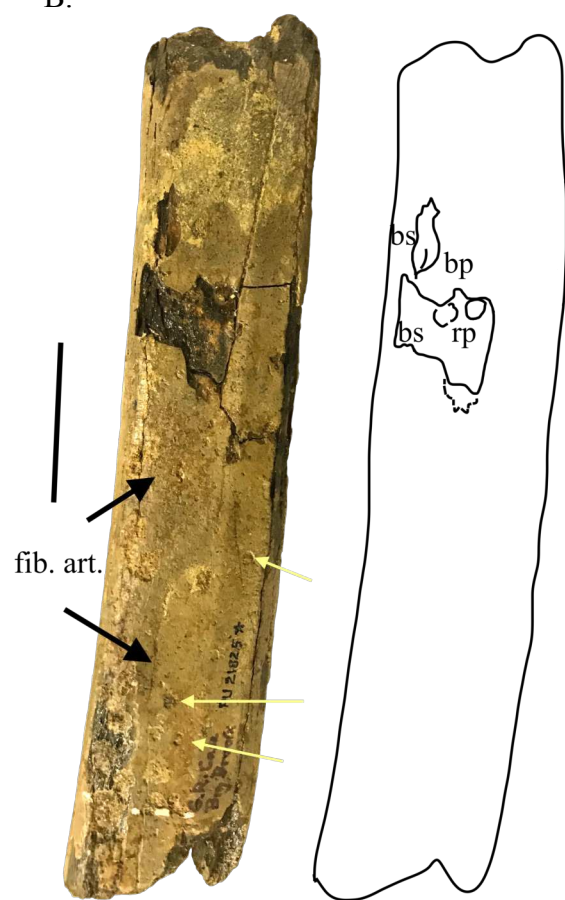
Partial tibia shaft with crocodyliform feeding marks and invertebrate traces

YPM VPPU.021825 in lateral (A), medial (B), and proximal (C) views, with closeups of crocodyliform feeding marks and possible invertebrate burrows on the lateral (D) and medial (E) faces of the bone. Scale bar = 50 mm (A-C), 10 cm (D-E). Black arrows indicate crocodyliform feeding marks; yellow arrows indicate possible invertebrate traces.

A.



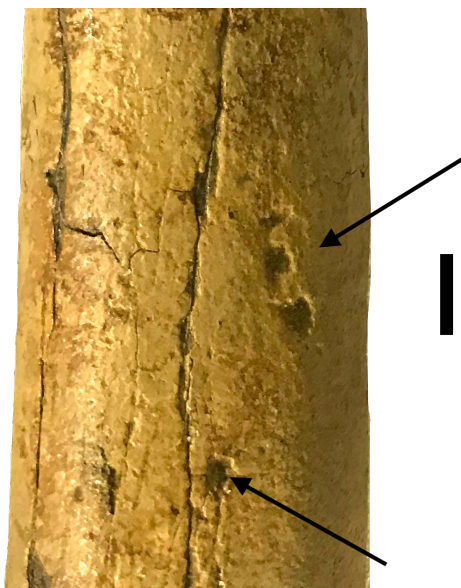
B.



C.



E.



F.

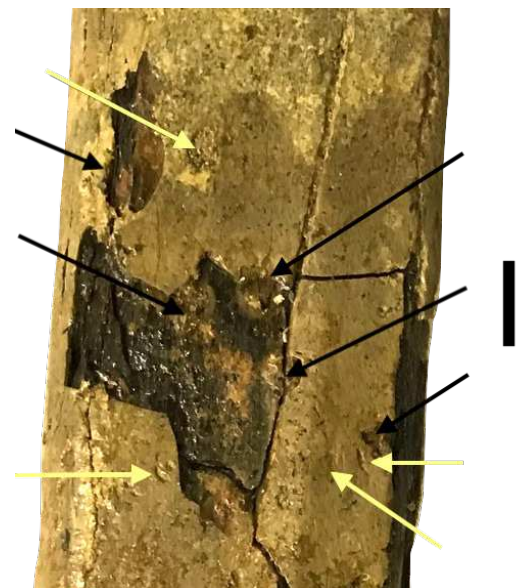


Figure 2(on next page)

Distal ornithomimosaur femur with shark feeding scores

YPM VPPU.022361 in lateral (A), medial (B), dorsal (C) ventral (D), and distal (E) views. Scale bar = 5 mm. Black arrows indicate shark feeding scores.

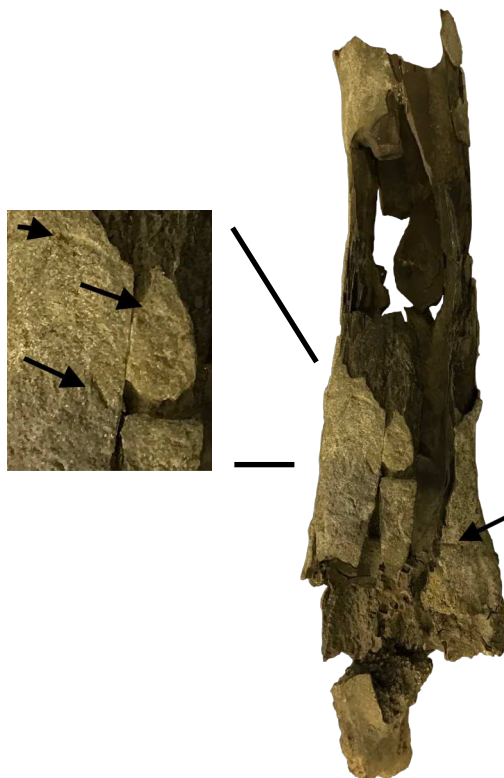
A.



B.



C.



D.



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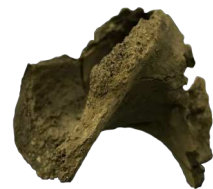


Table 1(on next page)

Measurements of theropod bones

Specimen	Proximodistal length	Distal mediolateral width	Distal dorsoventral width	Circumference at midshaft	Reference
YPM VPPU. 021825	222 mm	n/a	n/a	152 mm	this paper
YPM VPPU. 022361	290 mm	75 mm	59 mm	149 mm	Baird (1986), this paper

Table 2 (on next page)

Measurements of crocodyliform and shark feeding traces

Bite mark	Length	Width
Proximalmost lateral (YPM VPPU.021825)	3 mm	1 mm
Second proximalmost lateral (YPM VPPU.021825)	4 mm	3 mm
Second distalmost lateral (YPM VPPU.021825)	5 mm	4 mm
Distalmost lateral (YPM VPPU.021825)	4 mm	3 mm
Bisected medial (YPM VPPU.021825)	10 mm	6.5 mm
Jagged medial (YPM VPPU.021825)	6 mm	5 mm
Rounded medial (YPM VPPU.021825)	6 mm	6 mm
Proximalmost (YPM VPPU.022361)	9 mm	1 mm
Second proximalmost (YPM VPPU.022361)	6 mm	1 mm
Middle (YPM VPPU.022361)	5 mm	0.5 mm
Distalmost (YPM VPPU.022361)	4 mm	1 mm