Non-avian theropod phalanges from the marine Fox Hills Formation (Maastrichtian), western South Dakota, USA

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We report here the first dinosaur skeletal material described from the marine Fox Hills Formation (Maastrichtian) of western South Dakota. One find consists of a single theropod pedal phalanx recovered from the middle part of the Fairpoint Member in Meade County, South Dakota. Comparison with pedal phalanges of other theropods suggests strongly that it is a right pedal phalanx III-2 from a large ornithomimid. The bone comes from massively bedded and cross-bedded marine sands containing small, discontinuous, lenticular lag deposits and large hematitic concretions and concretionary horizons. Associated fossils include osteichthyan teeth, fin spines and otoliths, and abundant teeth of common Cretaceous nearshore and pelagic chondrichthyans. Leaf impressions and other plant debris, blocks of fossilized wood, and *Ophiomorpha* burrows are also common. We interpret the depositional environment as a beachfront or nearshore sandbar subject to tidal flux and frequent storms, and lying close to a river distributary. Orthogonal cracks in the cortical bone, and the absence of shark bite marks or other signs of marine scavenging activity suggest that the bone has a complex taphonomic history involving reworking into this marine setting long after post-mortem exposure in a more terrestrial depositional environment. The Fairpoint bone bed probably lies within the *Hoploscaphites nicolletii* Ammonite Zone of the early Late Maastrichtian, and would thus have an approximate age of 69 Ma. We also report the presence of an undescribed Fox Hills theropod phalanx, attributable to a medium-bodied non-avian theropod, in the collection of the Yale Peabody Museum. The Yale specimen is from the Iron Lightning Member in Ziebach County, SD. It comes from a marginal marine depositional environment similar to that of the Fairpoint bone, and appears to have a similar taphonomic history, but it is somewhat younger in age than the Fairpoint specimen.

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ABSTRACT: We report here the first dinosaur skeletal material described from the marine Fox Hills Formation (Maastrichtian) of western South Dakota. One find consists of a single theropod pedal phalanx recovered from the middle part of the Fairpoint Member in Meade County, South Dakota. Comparison with pedal phalanges of other theropods suggests strongly that it is a right pedal phalanx III-2 from a large ornithomimid. The bone comes from massively bedded and cross-bedded marine sands containing small, discontinuous, lenticular lag deposits and large hematitic concretions and concretionary horizons. Associated fossils include osteichthyan teeth, fin spines and otoliths, and abundant teeth of common Cretaceous nearshore and pelagic chondrichthyans. Leaf impressions and other plant debris, blocks of fossilized wood, and *Ophiomorpha* burrows are also common. We interpret the depositional environment as a beachfront or nearshore sandbar subject to tidal flux and frequent storms, and lying close to a river distributary. Orthogonal cracks in the cortical bone, and the absence of shark bite marks or other signs of marine scavenging activity suggest that the bone has a complex taphonomic history involving reworking into this marine setting long after post-mortem exposure in a more terrestrial depositional environment. The Fairpoint bone bed probably lies within the *Hoploscaphites nicolletii* Ammonite Zone of the early Late Maastrichtian, and would thus have an approximate age of 69 Ma. We also report the presence of an undescribed Fox Hills theropod phalanx, attributable to a medium-bodied non-avian theropod, in the collection of the Yale Peabody Museum. The Yale specimen is from the Iron Lightning Member in Ziebach County, SD. It comes from a marginal marine depositional environment similar to that of the Fairpoint bone, and appears to have a similar taphonomic history, but it is somewhat younger in age than the Fairpoint specimen.

INTRODUCTION

The Fox Hills Formation is a silty to sandy, fossiliferous nearshore to onshore deposit of Maastrichtian age that separates the marine shales of the Pierre Formation from the overlying terrestrial, dinosaur-rich Hell Creek and Lance formations of the Late Maastrichtian. In South Dakota, the Fox Hills Formation is exposed along a sinuous outcrop belt that curves around the northern and western flanks of the Black Hills (Figure 1A). To the east of the Black Hills lie two Fox Hills outliers, separated from the main trend of Fox Hills exposures, and from each other by erosion of the Cheyenne River and its tributaries. These outliers are referred to here as the Fairpoint-Enning area (green in Fig. 1A) and the Badlands National Park area (red in Fig. 1A). In the Fox Hills Type Area (blue, Fig. 1A), and in its extension in North Dakota, the lower part of the Fox Hills Formation (Trail City and Timber Lake members) is interpreted as a wedge of marine sand and silt prograding southwestward across the western interior basin (Waage 1961; Waage 1968; Landman and Waage, 1993). The sandy upper unit of the Type Area Fox Hills Formation (Iron Lightning Member) and the sandy Fox Hills exposures to the west of the Type Area represent the eastward and southeastward progradation of deltaic and shoreline deposits, referred to as the Sheridan Delta in Wyoming and Montana by Gill and Cobban (1973). These patterns of sediment migration are associated with the final closing of the Western Interior Seaway during the Late Maastrichtian and Early Danian (Waage, 1968; Erickson, 1969; Gill and Cobban 1973). Although terrestrial, lignitic horizons occur in the Fox Hills Formation of South Dakota (Waage, 1961; 1968; Black, 1964; Pettyjohn, 1967), this unit is primarily composed of marine sediments containing a macrofauna dominated by marine invertebrates, particularly gastropods (Erickson, 1974), bivalves (Speden, 1970; Erickson, 1978), and ammonites (Landman and Waage, 1993).

Remains of terrestrial animals, and dinosaurs in particular, are only rarely recovered from the Fox Hills Formation, even from its terrestrial beds. Hoganson et al. (2007) describe small theropod tooth fragments recovered from sites in the Bullhead lithofacies of the lowermost Iron Lightning Member in southcentral North Dakota. Waage (1968, p.127 and again on page 133) mentions a similar collection of fragmentary dinosaur remains, primarily tooth and claw fragments, from a channel deposit in the Colgate lithofacies of the Iron Lightning Member in the Fox Hills Type Area of northcentral South Dakota. In his paper erecting the Fairpoint and White Owl Creek members as formal units of the Fox Hills Formation in the Fairpoint-Enning area of western South Dakota, Pettyjohn (1967) mentions anecdotally that he encountered dinosaur bones in the middle part of the Fairpoint Member ("a few dinosaur and turtle bones as well as shark teeth were found throughout this unit", Pettyjohn, 1967, pg. 1364). He did not describe this material, however. The fate of Pettyjohn's Fox Hills dinosaur material is unknown, and as far as can be discerned, it does not appear that it was retained for future study.

In this paper we describe two small theropod phalanges from marine beds of the Fox Hills Formation. The first of these is from the Fairpoint Member in the Fairpoint-Enning area of western South Dakota (Fig. 1A), recovered as a by-product of earlier work by one of us (JAC) on fossil fish occurring in these same beds (Becker et al., 2004; 2009). The second is from a small assemblage of undescribed dinosaur material reported by Waage (1968) from the Iron Lightning Member in Ziebach County, South Dakota, about 190 km northeast of the Fairpoint locality (Fig. 1A), and now deposited in the vertebrate paleontology collections of the Yale Peabody Museum. Given the overall rarity of dinosaur remains in the Fox Hills Formation, particularly in western South Dakota, a formal description of these bones is warranted.

REPOSITORIES

The specimen from the Fairpoint-Enning area of South Dakota described here has been deposited in the vertebrate paleontology collections of the Denver Museum of Nature and Science (DMNS, formerly DMNH), Denver, CO, USA, and is identified by the catalogue number: DMNH EPV.138575. The specimen from the Fox Hills type Area in Ziebach County, South Dakota, is in the Yale Peabody Museum of Natural History (YPM), New Haven, CT, USA, and carries the catalogue number: YPM VP.061705.

COLLECTING LOCALITIES

DMNH EPV.138575: Specimen DMNH EPV.138575 was collected in Section 35, T7N, R14E (DMNH loc. 19383), about 13 km southeast of Enning, southeastern Meade County, South Dakota (Fig. 1B). This is the same site that yielded chondrichthyan teeth described in Becker et al., (2004) and osteichthyan remains detailed in Becker et al. (2009). DMNH EPV.138575 was recovered from a soft, laminated, well-sorted sandstone, white to tan in color, exposed near the top of a hillside above Pine Creek (Fig. 2). The sandy beds form pedestals arrayed beneath a dense pattern of hard, well-cemented, reddish-brown hematitic concretions, some up to 3 m in diameter. The concretions are ovoid in shape and coalesce in places, forming well defined horizons resistant to weathering and erosion. The sandstone is massively bedded, with hummocky, high-angle tangentially cross-stratified beds occurring at some horizons below the fossil beds (Fig. 3A). Some smaller fossils, including the teeth and other piscine material figured in Becker et al. (2004; 2009), occur in small, discontinuous, lenticular, pebbly lags visible in the sandstone pedestals (Fig. 3B). Many of the teeth are sediment polished and missing delicate crown and root elements. However, most small fossils are found weathered out of the sandstone and lying in the piles of loose sand distributed around the bases of the pedestals or in the debris mounds of harvester ant colonies located in the outcrop area (Becker et al. 2004). DMNH EPV.138575 was found lying in situ, and parallel to bedding, in the sandstone about a meter to the right of the lag shown in Figure 3B. *Ophiomorpha* burrows (Fig. 3C) are found both in the soft sand as well as in the hard concretions. Leaf impressions (Fig. 3D) and plant debris occur within the concretions overlying the phalanx horizon, and small blocks of fossil wood are scattered throughout the loose sand at the base of the pedestals.

YPM VP.061705: Waage (1968) indicates that specimen YPM VP.061705 was found in Sec. 33, T14N; R19E, Ziebach County, SD (YPM locality 74). The YPM specimen comes from Waage's (1968) type section of the Iron Lightning Member where it was measured in the SW corner of a drainage divide in the badlands located to the east of the gravel road running northward from Highway 212 to the village of Iron Lightning near the Moreau River. Waage (1968, p. 133) describes the Colgate lithofacies sand body containing YPM VP.061705 as a sandy, very fine to medium grained subgraywacke about 12 m thick, which weathers grayish white. Present are thin bands of iron stained shale and some carbonaceous laminae. Cross bedding is prominent in these beds. Also common are brown-colored ovoid concretions up to 4 m long. The basal portion of the unit contains rich fossil lenses and channel cuts preserving *Corbicula*, *Crassostrea*, *Anomia,* and fish teeth, primarily of the ray *Myledaphus bipartitus*. Also present are otoliths, wood fragments, mammal teeth, and fragmentary dinosaur remains. The latter consists of broken hadrosaur, ceratopsid, and theropod teeth, fragmentary theropod claws, and YPM VP.061705. In his measured Iron Lightning type section, Waage (1968, pg. 133) indicates that this channel cut dinosaur horizon in the Colgate lithofacies lies about 14 m below the base of the overlying Hell Creek Formation.

GEOLOGIC SETTING

DMNH EPV.138575: Pettyjohn (1967) recognized two stratigraphically distinct members in the Fox Hills Formation in the Fairpoint-Enning area of western South Dakota: the Fairpoint Member and the White Owl Creek Member. The Fairpoint Member, which lies on top of the Pierre Shale, is the lower of the two members. It is about 50 m thick and consists primarily of light-colored marine sands containing channel incisions, cross beds, with occasional horizons of dark, hematitic concretions. The uppermost part of the Fairpoint Member takes on a distinctly continental character in that it contains numerous lignite beds (the Stoneville Lithofacies of Pettyjohn (1967)). The White Owl Creek Member consists of massively bedded sands with large iron stained concretions and an upper unit of shales, silts, and sands, brightly colored by post-depositional paleosol development (Retallack, 1983; Jannett and Terry, 2008). Because our bone locality (Fig. 2) lies near the top of a hill, beds significantly higher in the sequence than the bone horizon have been removed by erosion at our recovery site.

The theropod site discussed here lies in the Fairpoint Member, about 40 m above the contact with the Pierre Shale (Figure 4). Pettyjohn (1967) states that his enigmatic dinosaur bones were found in a channel cut at the contact between what he considered the lower and middle parts of the Fairpoint Member. The approximate stratigraphic position of this bone bearing channel, about 20 m below our theropod site, is also indicated in Figure 4. However, the actual site of Pettyjohn's (1967) bone discovery is about 45 km northwest of our site.

YPM VP.061705: Waage (1968) defines the Fox Hills Formation in the north central part of South Dakota (the "Type Area" in Corson, Dewey, and Ziebach Counties) as consisting of the Trail City, Timber Lake, and Iron Lightning Members, the latter of which Waage (1968) created by combining two sandy lithofacies characteristic of the upper part of the Fox Hills Formation in the Type Area. Speden (1970) and Landman and Waage (1993) used this tripartite stratigraphic framework as the basis of their investigations of the Fox Hills bivalve and ammonite faunas. The Trail City is the lowermost of these members and according to Waage (1968) its thickness varies from about 21 m in the eastern part of the type area to about 70 m in the west. It consists primarily of fine clayey silt and contains richly fossiliferous concretionary horizons (Waage, 1968, figs. 24, 25 26). The Trail City Member is distinguished from the Pierre Shale below it by its higher silt content and the presence of jarosite beds in many localities.

The Timber Lake Member consists primarily of sandstone locally variable in grain size, clay content and bedding. It too contains horizons preserving abundant fossil-rich concretions. The Timber Lake Member also varies in thickness across the type area. More than 30 m thick in central Dewey County, it rapidly pinches out westward and is no longer present in western Dewey County (Waage, 1968, fig. 20). The contact of the Timber Lake Member with the Trail City Member below tends to be gradational, but southwestward in the Type Area the contact can often be recognized in terms of distinctive jarosite beds. Together with the Trail City Member, the Timber Lake Member represents a wedge-shaped sand body migrating southwestward into the shallow Western Interior Seaway near the close of the Cretaceous (Waage, 1968; Landman & Waage, 1993).

As conceived by Waage (1968), the Iron Lightning Member, the uppermost of the three Fox Hills members, consists of two contrasting sandy lithofacies, both of which differ from the sandy, clayey members of the Fox Hills Formation below it. The Bullhead Lithofacies consists primarily of finely bedded sand and silty clay usually having a brown color, while the Colgate Lithofacies is a white to gray, lithic sandstone commonly occurring in lenticular bodies often showing prominent cross-bedding and large, often dark colored, ovoid concretions. It also contains channel cuts, often with coarse debris, including fossils, preserved in the base, and, as described above, it is in one of these channel deposits about 14 m below the base of the overlying Hell Creek Formation, in which YPM VP.061705 was collected (Waage, 1968, pg. 133). Although the Bullhead Lithofacies occurs at the base of the Iron Lightning Member, and beds of the Colgate Lithofacies at the top of this member, Waage's (1968) stratigraphic sections from different parts of the Type Area (e.g., Waage, 1968; Figs 10, 25, and 26; Landman and Waage, 1993; Fig. 3) show that sand bodies of the two lithofacies are interspersed irregularly throughout the middle parts of the Iron Lightning Member. Lithologically, the Iron Lightning Member resembles Pettyjohn's (1967) Fairpoint Member in western south Dakota, and probably represents the later eastward migration of the Sheridan Delta near the close of the Maastrichtian rather than the westward advance of sedimentation of the Trail City and Timber Lake members.

GEOLOGIC AGE

DMNH EPV.138575: The absence of distinctive, time-indicative fossils, ammonites in particular, in the Fox Hills Formation of the Fairpoint-Enning area of South Dakota has historically been a major impediment to building a solid understanding of Fox Hills age relationships in this area. It also obfuscates correlation of Fairpoint Area lithology with that of the Type Area – a point recognized by both Waage (1968) and Pettyjohn (1967). Becker at al. (2004) suggest that in view of the eastward progression of Fox Hills deposition in western South Dakota, the middle to upper part of the Fairpoint Member near Enning in which DMNH EPV.138575 was preserved, is most likely time correlative to the lower parts of the Fox Hills Formation in its type area to the northeast. This would imply that the Fairpoint Member lies within the time interval represented by the *Hoploscaphites nicolletii* Ammonite Zone as defined in the Fox Hills type area by Landman and Waage (1993). Pettyjohn (1967) states that in the Fairpoint-Enning area the base of the Fox Hills Formation lies about 7 m above the *Baculites clinolobatus* Ammonite Zone in the uppermost Pierre Shale. In the Fox Hills type area, the base of the Fox Hills Formation is about 80 m above the *B. clinolobatus* Zone (Landman and Waage, 1993). These differences in relative positioning of the Fox Hills/Pierre contact, as noted in Landman et al. (2013, Fig. 5), suggest to us that the middle to upper Fairpoint Member in the Fairpoint-Enning area corresponds to the lower part of the *H. nicolletii* Zone in the Fox Hills Formation Type Area. We interpret these observations to mean that the Fairpoint horizon from which our specimen derives is from the lower part of the upper Maastrichtian sequence in western South Dakota. Cobban et al. (2006) and Merewether et al. (2011) record a radiometric age of 69.59±0.36 Ma for the *B. clinolobatus* Zone. More recently, Lynds and Slattery (2017) date the *B. clinolobatus* Zone at 70.08±0.37 Ma. Their data also indicate that the base of the *H. nicolletii* Zone has an age of about 69.3 Ma. This would suggest that the approximate age of DMNH EPV.138575 is on the order of about 69 Ma.

YPM VP.061705: The fact that the geologic age of Fox Hills beds rises to the east in South Dakota means that the age of the Yale specimen Waage (1968) recovered in the Fox Hills Type Area is likely to be younger than the Fairpoint specimen even though both occur in sandy Colgate style lithologies. YPM VP.061705, as reported by Waage (1968), was found at the base of a channel cut in the Iron Lightning Member about 14 m below its contact with the overlying Hell Creek Formation. In the type area, the *H. nebrascensis* Ammonite Zone, which overlies the *H. nicolletii* Zone, extends from just below the top of the Timber Lake Member, through the Iron Lightning Member, and into the overlying Hell Creek Formation where remains of the signature species, *H. nebrascensis*, have been found in the Breien Member of the Hell Creek Formation (Hartman and Kirkland, 2002; Landman, in Hoganson and Murphy, 2002; Landman, 2022, personal communication). Since the Breien Member lies about 2 to 9 m above the contact with the Fox Hills Formation (Hoganson and Murphy, 2002), the top of the *H. nebrascensis* Zone is about 16 to 23 m above the Iron Lightning Member horizon containing YPM VP.061705. This places YPM VP.061705 squarely in the *H. nebrascensis* Zone, and thus makes it significantly younger than DMNH EPV.138575. How much younger is more difficult to determine due to geographically variable thicknesses and ages of the beds in question. However, magnetostratigraphy provides a clue. The magnetostratigraphy data of Hicks et al. (2002, Figs. 11, 13) from southwestern North Dakota and the data of Lund et al. (2002; Fig. 10) from southcentral North Dakota, suggest that the base of the C30n polarity chron, which Lynds and Slattery's (2017) range data indicate to be about 68 Ma, lies about 10 m below the Hell Creek/Fox Hills contact. This is roughly the position of the bed containing YPM VP.061705 (14 m below the Hell Creek/Fox Hills contact). Thus, the age of this bone would probably be in the range of slightly more than 68 Ma, or nearly 1 Myr younger than that of DMNH EPV.138575

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen 1842 *sensu* Padian and May 1993

Theropoda Marsh, 1881 *sensu* Gauthier 1986

Tetanurae Gauthier, 1986 *sensu* Sereno et al. 2005

Coelurosauria von Huene, 1914 *sensu* Sereno et al. 2005

Description. – **DMNH EPV.138575**: This specimen is relatively robust and proximodistally elongate, with a preserved length of 80 mm. For a list of measurements, see Table 1. Its proximal dorsoventral and mediolateral widths are slightly greater than its distal dorsoventral and mediolateral widths. The proximal articular facet is concave and subtriangular in proximal outline and overgrown with framboidal pseudomorphic (pyrite) hematitic concretions. These concretions conceal detailed morphological features over much of the proximoventral portion, and where mechanically removed dorsally, have invaded and dissolved much of the cortical surface and dorsal morphology. Similarly, the distal articular facet, including the distal-most section of the condyle, has been obliterated by erosion, likely upon exhumation. We suspect that if the distal condyle were intact, the minimum length of the phalanx would likely be closer to 85mm, and perhaps even greater.

The shaft is arched ventrodorsally and slightly mediolaterally constricted just proximal to the plane corresponding with the arch's apex. In dorsal and ventral views, the shaft appears very slightly curved toward the larger collateral ligament fossa (here tentatively identified as the medial fossa), and neither proximal nor distal articular areas expand laterally. Just proximoventral to the larger (medial) ligament fossa, there is a slight protuberance that extents to the ventral surface of the bone. The shaft is oval in cross section, and in medial and lateral views, broadens toward the proximal end, terminating in framboidal hematitic concretionary growths. Apart from longitudinal and transverse fractures and some spalling of the dorsal cortex, the shaft is in better condition than both distal and proximal ends. The ventral surface of the specimen is moderately flattened and slightly asymmetrical. Proximally, the ventral surface includes two parallel plantar ridges running longitudinally towards the proximal facet. The medial of the two ridges is confluent with a subtriangular, rugose plantar surface. Distally, the ventral surface is weakly indented with a circular post-condylar depression. The dorsal surface of the shaft features a relatively rounded, gently medially curved ridge that runs longitudinally, becoming more exaggerated toward the proximal end. In dorsal view, the proximal facet is notably asymmetrical, sloping medially. A shallow depression of the extensor fossa is located dorsally, just behind the distal condylar surface.

The distal end is subrectangular in cross section, bearing a smooth, rounded articular condyle where not lost to diagenesis. The ventral margins of the distal condyle exhibit some pitting where true rugosities are apparent. The lateral collateral ligament pits are well developed, asymmetrical, teardrop shaped, relatively deep, and large, the medial pit being significantly larger than the other. Although some erosion has occurred, there is no indication that the dorsal surface of the condyle is significantly narrower than the ventral surface, thus the collateral fossae are not clearly visible in dorsal view. In addition, there is a very slight oval depression just distal of the proximal articulation facet on what we here identify as the lateral side (the side featuring the smaller ligament fossa).

Comparisons. **DMNH EPV.138575:**. The Fairpoint phalanx shares similarities with those reported from various tyrannosaurid taxa. These include: a slightly sloping long axis, ventral rugosities near the proximal articular facet and an arched ventral surface in medial and lateral views (Brochu, 2003); a shallowly concave proximal facet (evident in proximal phalanges; Lambe, 1917); deep and asymmetric collateral ligament fossae (a trait shared by all phalanges apart from those belonging to digit III, which are equal in size (Lambe, 2017; Brochu, 2003, figs. 107 and 108; Brusatte et al., 2012); and a relatively shallow extensor pit (Brusatte et al., 2012, fig. 80; Brochu, 2003, fig. 105). However, there are also dissimilarities, the most glaring ones of which are the relatively small size (smaller than all but the distal most phalanges of digit IV in the adult *Tyrannosaurus rex*, see Brochu, 2003) and the lack of expanded distal and proximal articular regions relative to the shaft in dorsal and ventral views (Brochu 2003). Moreover, the ratio of proximodistal length to mediolateral midshaft width is larger than 3, if the abraded distal condyle is taken into account, a value greater than that identified for Tyrannosauridae (Brusatte, 2010, SOM). All in all, the Fairpoint phalanx appears slightly more gracile than the pedal phalanges of adult tyrannosaurs known from North America of a similar stratigraphic age. We suspect that this could be due to ontogenetic variation, and that DMNH EPV.138575, if indeed tyrannosaurid in nature, could potentially have belonged to a subadult individual. Its size is consistent with the phalanges described from the Upper Cretaceous Horseshoe Canyon tyrannosaurid of Alberta, Canada (Mallon et al., 2020, Table 1). In fact, DMNH EPV.138575 bears striking similarities with pedal phalanx II-2 of the Horseshoe Canyon tyrannosaurid in that both have a shallow extensor fossa, deep collateral ligament pits, and a minimally mediolaterally constricted and slightly curved diaphysis (Mallon et al., 2020, fig. 16). However, the Horseshoe Canyon specimen exhibits a proximally projecting dorsal lip at the proximal articular facet, a feature that is not apparent in our specimen but may have been destroyed as the bone shows damage here. As observed in the phalanges of many tyrannoaurids, the distal condyle in the Horseshoe Canyon specimen narrows dorsally, revealing the collateral fossae in dorsal view and resulting in a subtrapezoidal, rather than subrectangular, cross section.

DMNH EPV.138575 also possesses morphological features comparable to those observed in the proximal pedal phalanges of various ornithomimids. These characteristics, which are also represented in tyrannosaurids, include a shallowly concave proximal articular facet, (Kobayashi and Barsbold, 2005; Cullen et al., 2013; Osmólska et al., 1972, Chinzorig et al. 2017), a shallow extensor fossa (Shapiro et al., 2003, fig. 1; Cullen et al.,2013, figs. 2 and 3; Sues and Averianov, 2016, fi.g 24; Claessens and Loewen, 2015, figs. 5, 6 and 8) and deep and distinct collateral ligament fossae (Smith and Galton, 1990; Kobayashi and Barsbold, 2005; Shapiro et al., 2003, fig.1). Interestingly, DMNH EPV.138575 shares similarities specifically with phalanx II-1 of an unnamed ornithomimid from Uzbekistan's Late Cretaceous Bissekty Formation (Sues and Averianov, 2016, fig. 24) and *Ornithomimus velox* of the Late Maastrichtian Denver Formation (Claessens and Loewen, 2015; figs. 5, 6 and 8). These include a slightly deflected ridge running longitudinally across the dorsal surface; deep, asymmetrical collateral ligament pits; a slight protuberance emanating just proximoventrally from the larger ligament pit; and a shallow extensor fossa. However, in DMNH EPV.138575, the proximodistal length is significantly greater (by about 30 mm) and the ventral ridges near the proximal facet are notably less pronounced, though possibly abraded. The most consistent placement based on overall morphology is a right phalanx III-2, comparing most closely with TMP2015.007.0315, an ornithomimid foot from the Dinosaur Park Formation of Alberta. Morphologically similar but more size-equivalent with our specimen is the pedal material belonging to unidentified members of Ornithomimidae recovered from a Late Cretaceous bone bed in Alberta, Canada (Cullen et al., 2013; figs 2 and 3), or *Beishanlong,* a giant ornithomimosaur from the Early Cretaceous of China (Makovicky et al., 2010; fig. 3). Other anomalously large ornithomimid elements are known from other Cretaceous deposits in the Western Interior or North America, including the Dinosaur Park Formation (Longrich, 2008), suggesting the presence of unidentified large-bodied taxa or upper body size limits beyond expectations based on more complete materials.

Because no other skeletal elements have been found associated with DMNH EPV.138575, and because some key morphological features are either destroyed or concealed by hematitic overgrowths, we cannot conclusively assign the element to a particular non-avian theropod clade. However, based on several morphological characteristics, size of the element, and stratigraphic age, we tentatively attribute the phalanx to a member of Coelurosauria, likely belonging to a large-bodied member of Ornithomimidae, specifically right pedal phalanx III-2.

Dinosauria Owen 1842 *sensu* Padian and May 1993

Theropoda Marsh, 1881 *sensu* Gauthier 1986

Tetanurae Gauthier, 1986 *sensu* Sereno et al. 2005

Coelurosauria von Huene, 1914 *sensu* Sereno et al. 2005

***Description.* – YPM VP.061705:** While relatively robust, phalanx YPM VP.061705 is significantly smaller than DMNH EPV.138575, with a proximodistal length of 44 mm (see Table 1 for additional measurements). The phalanx preserves much of its original surface, missing only the dorsal half of the proximal articular surface to breakage. A weak, vertical medial ridge divides the proximal articular cotyle into slightly concave medial and lateral portions. In proximal view, the articular surface appears sub-triangular to moderately pentagonal in cross-section, with the lateral sides nearly vertical (steep-sided). Ventrally on the proximal end, a broad lip-like asymmetrical flange projects medially. The proximoventral surface is planar, with two faint plantar ridges oriented longitudinally near the proximal facet indicated by a highly vascularized cortical surface. The shaft is moderately arched dorsoventrally and mildly pinched near the distal condyle. The proximal and distal areas are expanded relative to the shaft in dorsoventral but especially in mediolateral view. The distal articular condyle is divided into two highly asymmetrical distal hemi-condyles separated by a vertical sulcus. The medial hemi-condyle is dorsoventrally significantly larger than its lateral counterpart, dorsally thickened, and inclined dorsolaterally towards the sagittal midline. The lateral and medial ligament fossae are ellipsoidal, the medial being deeper and modestly visible in dorsal view. On the dorsal surface just proximal between both hemi-condyles, a relatively shallow extensor fossa is evident.

Macroscopically, YPM VP.061705 appears well-preserved. As in other vertebrate appendicular elements capped by cartilaginous soft tissues, the texture of the articular surfaces is distinctly rough contrasting the smooth, compact cortical surface of the shaft. Some mild pitting of the cortex is apparent but whether this is diagenetic or pathologic is unclear. Where the bone is spalled, the internal spongy tissue is porous, showing little to no diagenetic mineral infilling.

***Comparisons*. YPM VP.061705:** Because many morphological traits of pedal phalanges are shared by various coelurosaurian clades, particularly between the temporally relevant Ornithomimidae and Tyrannosauridae, it is difficult to attribute this single, isolated specimen to either group definitively. Nevertheless, because of its geographic and stratigraphic location, its general morphology and size, we cautiously assign YPM VP.061705, like DMNH EPV.138575, to Ornithomimidae, specifically left pedal phalanx II-2. Several attributes are consistent with pedal phalanx II-2 of CMN 12068 described by Cullen et al. (2013), including its width to length ratio, its pronounced proximoventral flange and its ginglymoid proximal articular facet (Cullen et al., 2013, fig. 2 C). Likewise, we see considerable similarities with pedal phalanx II-2 of a large lower Cretaceous ornithomimid from China's Ganzu province, such as deep medial ligament fossa, the significantly enlarged distal condyle relative to shaft diameter, a shallow extensor fossa, and overall shape and width to length ratio (Shapiro et al., 2003; fig. 1 C and D). Dissimilarities in pedal phalanx II-2 of the stratigraphically similar North American *Ornithomimus velox* indicate either a tentative assignment of YPM VP.061705 to Ornithomimidae, or reveal undocumented variation in pedal phalangeal morphology within the clade. Phalanx II-2 of *O. velox* is proximodistally and dorsoventrally more compressed than YPM VP.061705, with a notably shorter shaft; a less exaggerated distal condyle relative to shaft diameter; and shallower ligament fossae (Claessens and Loewen, 2015; fig. 8).

DISCUSSION

Depositional Environment of DMNH EPV.138575: Landman et al. (2013; Fig. 5) indicate that the western shoreline of the Western Interior Seaway (WIS) during the upper *H. nicolletii* Zone extended from SW to NE across South Dakota. Our collection site lay very close to, but on the seaway side, of the shoreline. They envision this shoreline as highly irregular and characterized by headlands, bays, estuaries, bars, and shoals, a view consistent with Hoganson et al.'s (2007) description of the shoreline in North Dakota, and that of Becker et al. (2004) for the paleoenvironment of the collection site itself.

While deposition in a shifting, unstable, sandy shoreface environment seems apparent, Becker et al. (2004) also note that except for the beds shown in Figure 2, from which their specimens, and DMNH EPV.138575, derive, fossils are uncommon above and below the bone horizon. This, together with the observation that our White Owl assemblage consists of mixed terrestrial, freshwater, and marine faunal elements, suggests that the fossiliferous beds at White Owl may represent a condensed section resulting from a short-lived transgressive event in an otherwise overall sea-level regression associated with the retreat of WIS waters at the close of the Cretaceous and the development of the Dakota Isthmus (Erickson, 1978; 1999). Similar mixed assemblages deriving in part from short term transgressive events, are known from the Atlantic Coastal Plain, such as in the Campanian Black Creek Group of North Carolina (Schwimmer, 1997); the Campanian Marshalltown Formation at Ellisdale, New Jersey (Brownstein, 2018); and in the Type Area Iron Lightning member of the Fox Hills Formation itself (Waage, 1968). The discovery of scaphite shell fragments in the overlying Hell Creek Formation (Hoganson and Murphy 2002; Hartman and Kirkland 2002) and Lance Formation (Jeletzky and Clemens, 1965) indicate that transgressive marine incursions are a feature of the waning phases of the WIS. Deposition of the bone bed at our White Owl bone locality was probably produced by a more transient, small-scale transgression than those observed in the continental Hell Creek or Lance Formations.

Depositional Environment of YPM VP.061705: The depositional environment preserving the Yale phalanx is essentially similar to the shallow, nearshore paleoenvironment in which the Fairpoint phalanx occurs. Waage (1968) regarded the Iron Lightning Member as the product of coastal, lagoonal, delta-topset deposits related to the eastward migration of the Sheridan Delta. Channels of Colgate lithology were cut into these deposits by currents flowing across them. Waage (1968) points out that the Yale phalanx was part of a basal channel accumulation containing terrestrial, freshwater, and nearshore marine fossils. Thus, there is the possibility that YPM VP.061705 is associated with a tidal or distributary channel associated with the deltaic setting then beginning to dominate the northern parts of the Western Interior. The depositional environment of YPM VP.061705 would appear, therefore, to have been somewhat more onshore as compared to that of DMNH EPV.138575.

Temporal Significance: The inferred age of 69 Ma for the horizons preserving DMNH EPV.138575 place it in a poorly-represented biochronological interval of the middle Maastrichtian, representing an interval within the poorly defined 'Edmontonian' NALMA. Contemporary Western Interior terrestrial faunas from this interval are known from the Prince Creek Formation of Alaska (Mull et al., 2003); the Wapiti (Unit 5; Fanti and Catuneanu, 2009) and Horseshoe Canyon (Tolman Member; Eberth and Braman, 2012) formations of Alberta; the North Horn Formation (Unit 1; Difley and Ekdale, 2002) of Utah; the Ojo Alamo Formation (Lucas et al., 2009) of New Mexico, the Javelina Formation (Lehman et al., 2006) of Texas; and possibly portions of the lower Laramie Formation of Colorado (Raynolds, 2002; Wilson et al., 2010). Many of these faunas preserve similar dinosaurian components, including hadrosaurid, ceratopsid, pachycephalosaurian, and ankylosaurian ornithischians, and tyrannosaurid, ornithomimid, oviraptorosaurian, and paravian theropods. The presence of an ornithomimid, or tyrannosaurid, is therefore not surprising, though it does underscore the potential significance of any terrestrial vertebrate remains from the Fox Hills Formation in understanding biotic distribution and diversity of the Western Interior during the Edmontonian.

Bone Taphonomy DMNH EPV. 138575: Apart from damage to the distal and proximal ends of the phalanx as a result of hematitic overgrowth, the bone does not appear to be abraded to any significant degree even though it was buried in what was clearly an unstable, shifting substrate. However, there are several longitudinal and transverse cracks in the cortical bone. Although some breakage occurs in acute or obtuse angles, the primary breakage pattern here appears to be orthogonal, at right angles. Such a pattern has been observed in the fracturing of dry bone, i.e., breakage that occurs in purely mineralized or permineralized bone after the loss of internal organic material (Johnson, 1985; Morlan, 1984; Villa and Mahieu, 1991). In a few places, slivers and flakes of cortical bone have spalled off the specimen. These features are clearly seen in Figure 5. This does not appear to be the result of predation or scavenging by sharks because the shape of the elongated, irregular outline of the cracks is inconsistent with the often arcuate repetitive incisions made by blade-like shark teeth as the shark shakes its head from side to side after biting down (Schwimmer et al., 1997; Everhart and Ewell, 2006; Becker et al., 2006). Moreover, the smooth surface of the bone precludes it having been digested in the gut of a predator, the result of which would have been an eroded, broken-down bone surface (Chin et al. 1998; Varricchio, 2001; Everhart, 2003, 2004; Everhart and Ewell, 2006; Schwimmer et al. 2015b). It is also possible such bone loss was due to the impact of large pebbles or other objects mobilized by storm or tidal flows, but the near absence of abrasion on the bone and the absence of large clasts in the sandstone argues against this alternative.

Small hematitic concretions adhere to the surface of the bone (Fig. 5). Two particularly evident hemispherical concretions, each about 1.5 cm in diameter, attach to the articulation surface at the proximal end of the bone (Fig. 5). The bone has a dark color where similar concretions have broken away from the bone surface on both proximal and distal extremities. In addition, smaller, flattened irregular concretions coat portions of the bone shaft and the surfaces of the collateral ligament pits. All of these concretions are composed of sedimentary grains, mostly quartz, cemented together and to the bone by microcrystalline hematite and probably other iron oxides as well. Pyrite crystals are not visible, although they were undoubtedly present when the concretions were forming diagenetically. The bone was recovered from clean sand well removed from any of the hematitic concretions or concretionary layers that occur in the outcrop (Figure 2), so that the formation of the bone concretions may reflect the localized microenvironment immediately surrounding the bone rather than more widespread parameters such as groundwater movements that created the large concretions and concretionary horizons.

Pyrite and iron oxides can replace organic material (Sawlowicz and Kaye, 2006; Canfield and Raiswell, 1991), and can form in and on fossil bone in various different ways (Pfretzschner, 2001, Bao et al.,1998). Decomposition of organic matter can nucleate concretions and spur their growth because of its effect on local pH and eH. The relative prominence of the concretions associated with articulation surfaces and ligament pits is interesting because it is these parts of the bone to which tendon and cartilage, which are soft tissues slow to decay, are attached. The concretions visible on DMNH EPV.138575 thus may mean that flesh still adhered to it when it was initially buried. Alternatively, these concretions could have precipitated on those surfaces favorable to the decomposition of the bone's more durable internal organic compounds. As is the case in most long bones (Bishop et al., 2018; Moreira et al. 2019), the cortex of pedal phalanges appears thickest along the shaft (where the mineral density is higher), whereas near the proximal and distal articulation surfaces the cortex progressively thins and the internal space is dominated by more vascular cancellous bone tissue whose mineral density is lower. Near or at the articulation surfaces these conditions (thin cortex and porous bone texture) would allow for easier access to bone internal organic material, such as collagen, enabling microbial decomposition, the byproducts of which (i.e., sulfide) if combined with dissolved iron could have precipitated pyrite in and on the bone. This form of pyritization would have occurred during the early diagenetic stages (Pfretzschner, 2001, 2004). During late diagenesis, the pyrite could have oxidized while near the surface to form the hematitic concretions evident today. However, if the hematitic concretions are, in fact, the product of the oxidization of pyrite formed from the decomposition of organic matter in or on the bone, the dry bone fracture pattern stands in direct taphonomic contrast, because it suggests the absence of organic material when breakage occurred. This would imply that pyritization took place either before fracturing or not by means of the decay of organic compounds. The mode of iron oxide formation was not further studied in this paper so that a more complete taphonomic history of DMNH EPV.138575 remains unresolved.

Bone Taphonomy YPM VP.061705: We do not attempt to interpret the taphonomy of the Yale bone in detail because we were unable to examine the specimen first-hand due to COVID-19 pandemic restrictions in force at the time of the writing of this article. However, the overall exceptional preservation of the external bone surface, preserving minute details of vascularization and soft tissue attachments, suggest rapid burial with minimal transport.

SIGNIFICANCE OF MARINE PRESERVATION OF DINOSAUR REMAINS

Preservation of dinosaur skeletal elements in Cretaceous estuarine and marine sedimentary rocks of North America is unusual but not unknown. Occasionally, such preservation is associated with a find of spectacular proportion as the discovery in 1858 of a partial hadrosaur skeleton from the marine Woodbury Formation, an offshore glauconitic marl of Campanian age, in Haddonfield, New Jersey (NJ), USA (Leidy, 1859a, 1859b; Foulke, 1859). This was the first partly articulated dinosaur skeleton recovered in the western hemisphere. Its discovery heralds the great American dinosaur rush of the late 19th and early 20th centuries involving such celebrated dinosaur hunters as E.D. Cope, O.C. Marsh, H.F. Osborn, and B. Brown.

More often, dinosaur skeletal material recovered from coastal settings is dissociated, disseminated and fragmentary. Yet, such occurrences can be of prime importance in identifying the dinosaur fauna inhabiting adjacent land masses. This is the case of the Ellisdale site in western Monmouth County, NJ, where erosion by Crosswicks Creek of the Campanian Marshalltown Formation, a sandy, glauconitic marine marl, has uncovered a numerically abundant and taxonomically diverse assemblage of dinosaur skeletal fragments derived from hadrosaurs and other ornithopods, and theropods, including dromaeosaurs, ornithomimosaurs, and tyrannosaurs (Weishampel and Young, 2006; Brownstein, 2018). These fossils, as well as other dissociated dinosaur remains from other units of the Cretaceous sedimentary record of the Atlantic and Gulf Coastal Plains (Baird and Hoerner, 1979; Schwimmer et al. 1993; Kiernan and Schwimmer, 2004; Carr et al., 2005; Ebersole et al. 2011; Schwimmer et al., 2015a; Farke and Phillips, 2017) and Great Plains (Mehl, 1931, 1936; Eaton, 1960; Everhart and Hamm, 2005; Liggett, 2005), impart a reasonably detailed picture of the dinosaur fauna inhabiting Appalachia, the somewhat isolated eastern portion of North America which was separated from western North America during much of the Cretaceous by the Western Interior Seaway (WIS).

The Cretaceous sedimentary record of dinosaur remains occurring in marine and estuarine settings of the WIS also has its spectacular finds, as for example the shark-bitten nodosaurid and hadrosaur bones described by Schwimmer et al. (1997) and Everhart and Ewell (2006), or the hadrosaur remains from the marine Bear Paw Shale first discovered by Douglass (1902), but not actually described until much later by Horner (1979). In his 1979 paper, Horner provides a listing of marine dinosaur finds for both the Western Interior and the eastern part of the USA, and points out the existence of a striking disparity in the abundance and diversity of eastern marine dinosaur occurrences as compared to those from the Western Interior. His tabulation shows that the Western Interior Cretaceous marine record contains fewer reports of far less dinosaur material than do descriptions of time-equivalent strata from the Atlantic and Gulf Coastal Plains. Horner (1979) attributes this dichotomy, not to an inherent paucity of dinosaur remains in Western Interior marine rocks, but rather, to the remarkable richness of dinosaur assemblages preserved in the widespread terrestrial rocks of the adjoining western landmass of Laramidia, which he felt has drawn the attention of dinosaur workers to the terrestrial Campanian-Maastrichtian sequence. His view, with which we agree, was that the rocks of the WIS may represent a more valuable target for informative dinosaur research than has been so far appreciated. In contrast, except for the Arundel Clay, a localized paludal deposit in eastern Maryland (Kranz, 1998; Frederickson et al., 2018), Appalachia has no significant Cretaceous terrestrial sedimentary record, and thus the Appalachian marine sequence has perforce become the preeminent resource for dinosaur workers in the eastern and southern USA.

Horner's tabulation (Horner, 1979) shows that the known occurrences of Western Interior marine dinosaur preservation are numerically greatest along the southeastern margin of the Seaway, in the states of Mississippi, Missouri, and Arkansas, and thus probably derive from animals inhabiting Appalachia. A few mid-Seaway occurrences, representing more offshore depositional settings are also known from the Pierre Shale of South Dakota and the Niobrara Formation of Kansas. On the western side of the Seaway are several occurrences in the nearshore portions of the Bear Paw Shale of Montana and the Thermopolis Shale of Wyoming. These finds would presumably represent animals once living in Laramidia. Several additional discoveries of Laramidian dinosaurs preserved in Seaway rocks have been made since Horner published his tabulation, including hadrosaurs (Fiorillo, 1990; Lucas et al., 2006), a nodosaur (Brown et al., 2017), and a therizinosaur (Zanno et al., 2009).

Conspicuously missing from Horner's compilation is the Fox Hills Formation, a unit usually considered as the product of nearshore to coastal, and locally onshore, deposition along the western margin of the Seaway and shoreline of Laramidia for a large part of the Late Cretaceous (Waage, 1968; Erickson, 1974; Landman and Waage, 1993; Horner, 1989; Becker et al., 2004; Hoganson et al., 2007; Olariu et al. 2012). With Hoganson et al.'s (2007) broken tyrannosaurid and dromaeosaurid teeth fragments from sites in southcentral North Dakota, and now the Fox Hills pedal bones described here, the Fox Hills Formation can be added to the list of Western Interior marine units preserving remains of dinosaurs. The presence of these fossils in marginal marine Fox Hills sediments indicates that these theropods probably inhabited Western Interior shoreline environments, as Ostrom (1990) and others have suggested earlier. Moreover, as pointed out by Hoganson et al., (2007), the occurrence of these and other terrestrial animals preserved in Late Maastrichtian marginal Seaway sediments holds considerable promise in helping to interpret the complex depositional patterns and paleoenvironmental shifts that occurred during the waning of the Western Interior Seaway in the Late Maastrichtian.

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Figure 1

Locality Maps

(A) Exposure area of the Fox Hills Formation surrounding the Black Hills of western South Dakota, USA. Modified from Landman & Waage, 1993, Fig. 1. Outcrop areas of primary interest in the present paper are the Fairpoint-Enning Area (green) studied by Pettyjohn, (1967); Becker et al. (2004, 2009); the Badlands National Park area (red) studied by Chamberlain et al. (2001); Stoffer et al. (2001); Jannett & Terry (2008); Landman et al (2013); and the Fox Hills Type Area (blue) studied by Waage (1961; 1968); Speden (1970); and Landman and Waage (1993). Red Star – collection site of the theropod phalanx DMNH EPV.138575. White Star – collection site of the theropod phalanx YPM VP.061075. (**B)** Detailed map of White Owl, South Dakota, showing the location of DMNH EPV.138575 outcrop discussed here Denver Museum of Science and Nature locality number 19383). Modified from Becker et al., 2004, Fig. 1. North is toward the top of the page in both maps A and B.

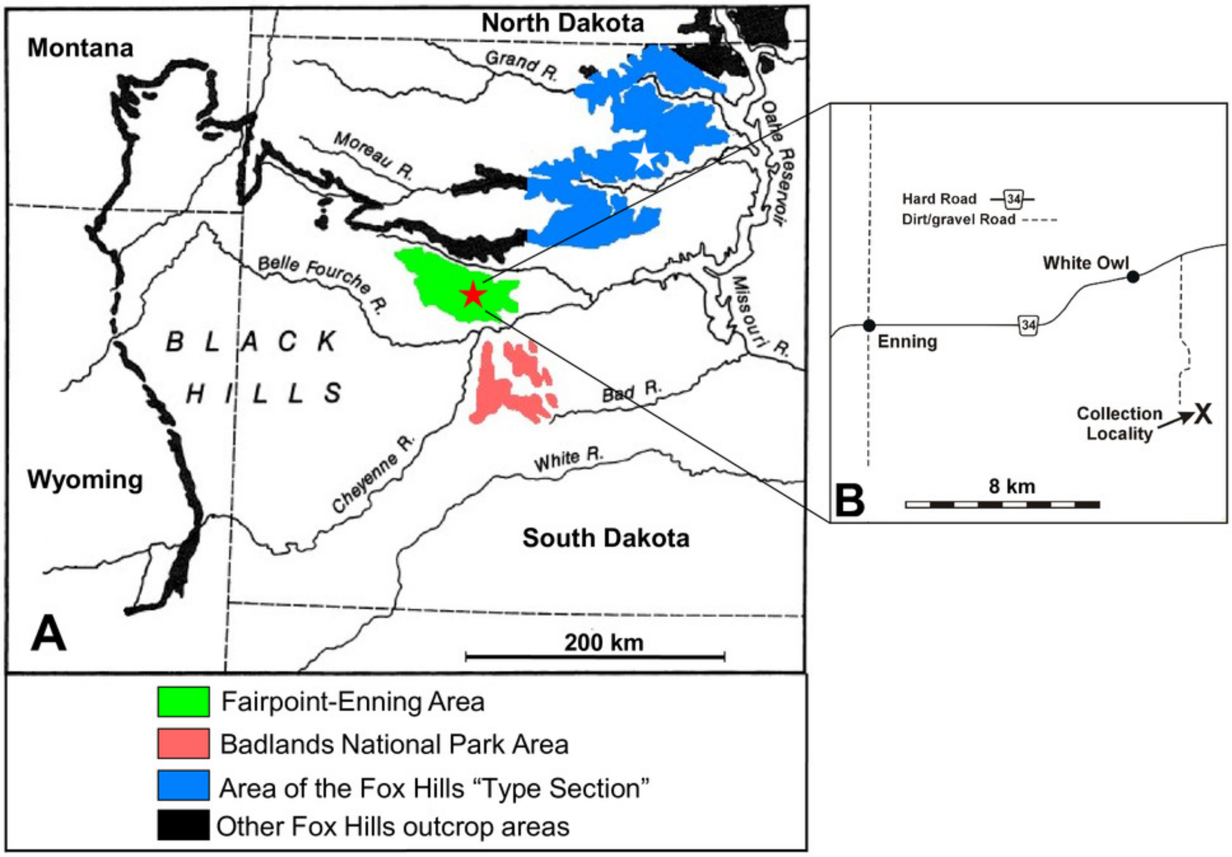
North Dakota
Montana
Grand R.
Moreau R.
Oahe Reservoir
Belle Fourche R.
B L A C K
H I L L S
Missouri R.
Bad R.
Cheyenne R.
White R.
Wyoming
South Dakota
A
200 km
Hard Road
34
Dirt/gravel Road
White Owl
Enning
Collection Locality
X
B
8 km
Fairpoint-Enning Area
Badlands National Park Area
Area of the Fox Hills “Type Section”
Other Fox Hills outcrop areas

Figure 2

White Owl outcrop of the Fairpoint Member yielding DMNH EPV.138575

the view is southwesterly from the top of the hill on which the outcrop occurs. The bone was recovered from a soft sandstone pedestal standing beneath a hard, hematitic concretion at the position marked by the white square. Photo credit: John Chamberlain

Figure 3

Sedimentary features and fossils of the White Owl theropod site

(A) Eroded sandstone block composed of hummocky and high-angle tangential cross-stratification; water bottle is 25 cm high. Modified from Becker et al. (2004, fig. 2B). **(B)** Pebbly, lenticular lag showing chondrichthyan tooth (arrow) eroding out of the sandstone; hand lens is 2 cm in diameter. Modified from Becker et al. (2004; fig, 2D). Theropod bone was found about a meter to the right of this lag. (**C)** *Ophiomorpha* burrow from a hematitic concretion, marker pen is 14 cm in length. (**D)** Positive and negative of leaf impression from a hematitic concretion. Scale bar = 2 cm. The specimen is probably a leaf fragment of the buckthorn, *Rhamnus salicifolius*, which is known from the Fox Hills Formation in North Dakota (Peppe et al. 2007). Photography by John Chamberlain

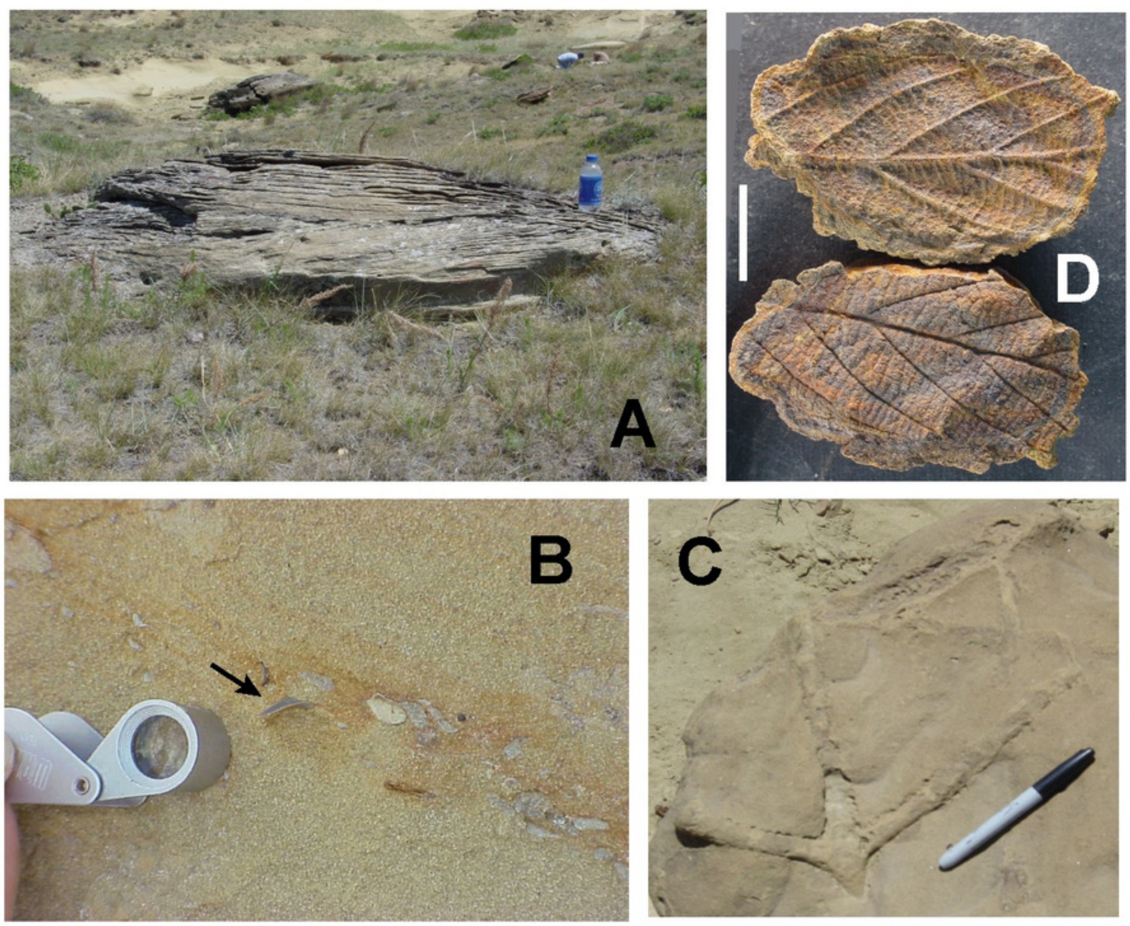

Figure 4

Stratigraphic column of the Fox Hills Formation in the Fairpoint-Enning area of western South Dakota.

(A) Stratigraphic horizon of the theropod phalanx described in this paper. (**B)** Stratigraphic horizon of the dinosaur bones anecdotally mentioned by Pettyjohn (1967). Scale bar = approximately 25 meters. This is a composite sketch modified from widely spaced localities studied by Pettyjohn (1967; Fig. 2); Stoffer et al. (2001; Fig. 13), Becker et al. (2004, Fig. 3), and Chamberlain et al. (2005, Fig. 6).

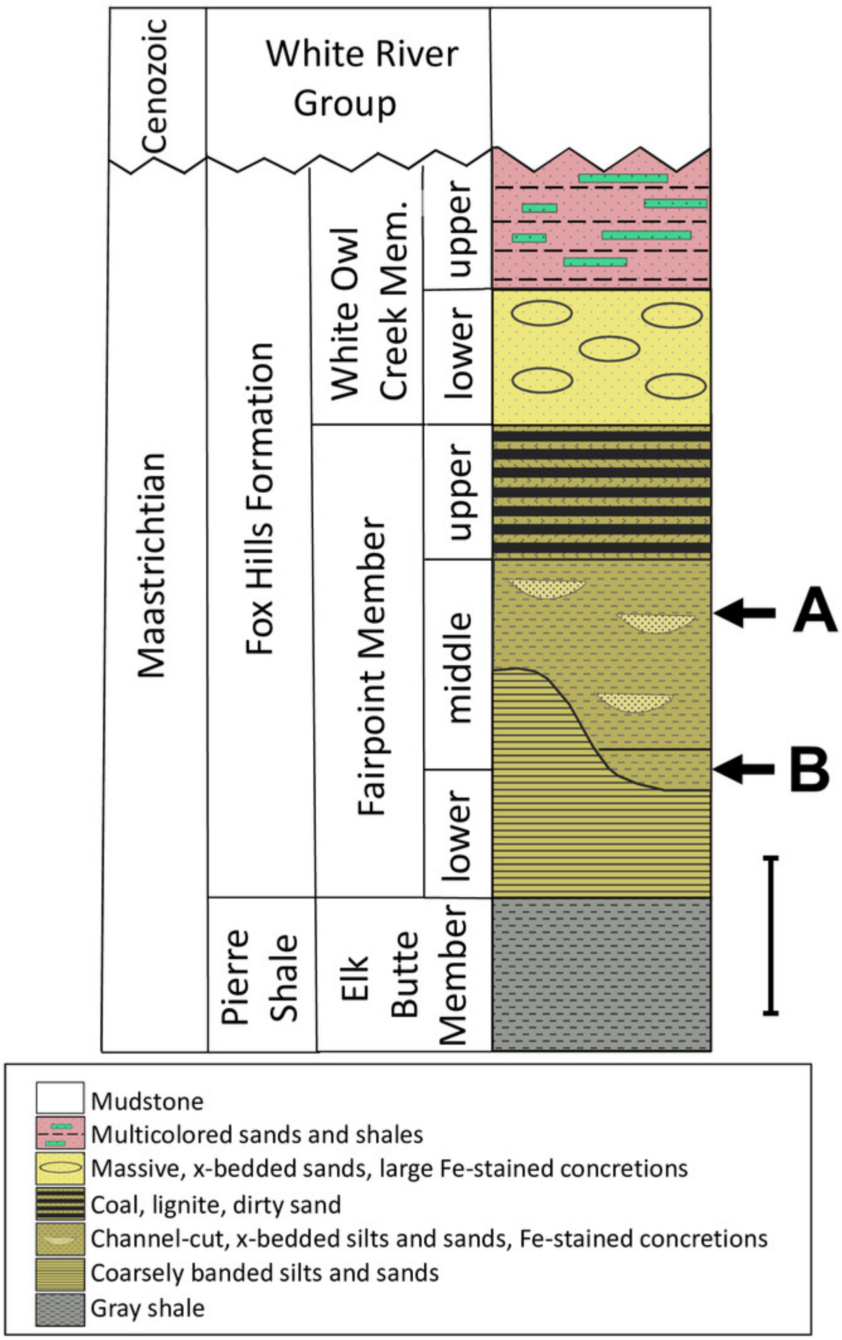
Cenozoic
White River Group
Maastrichtian
Fox Hills Formation
White Owl Creek Mem.
upper
lower
Fairpoint Member
upper
middle
lower
Pierre Shale
Elk Butte Member
A
B
Mudstone
Multicolored sands and shales
Massive, x-bedded sands, large Fe-stained concretions
Coal, lignite, dirty sand
Channel-cut, x-bedded silts and sands, Fe-stained concretions
Coarsely banded silts and sands
Gray shale

Figure 5

Fairpoint Member phalanx, White Owl, South Dakota; DMNH EPV.138575

(**A)** lateral, (**B**) dorsal, (**C**) distal, (**D**) medial, (**E**) ventral and (**F)** proximal views. Note that medial and lateral are tentative designations. Scale bar is 5 cm. Photography by Katja Knoll.

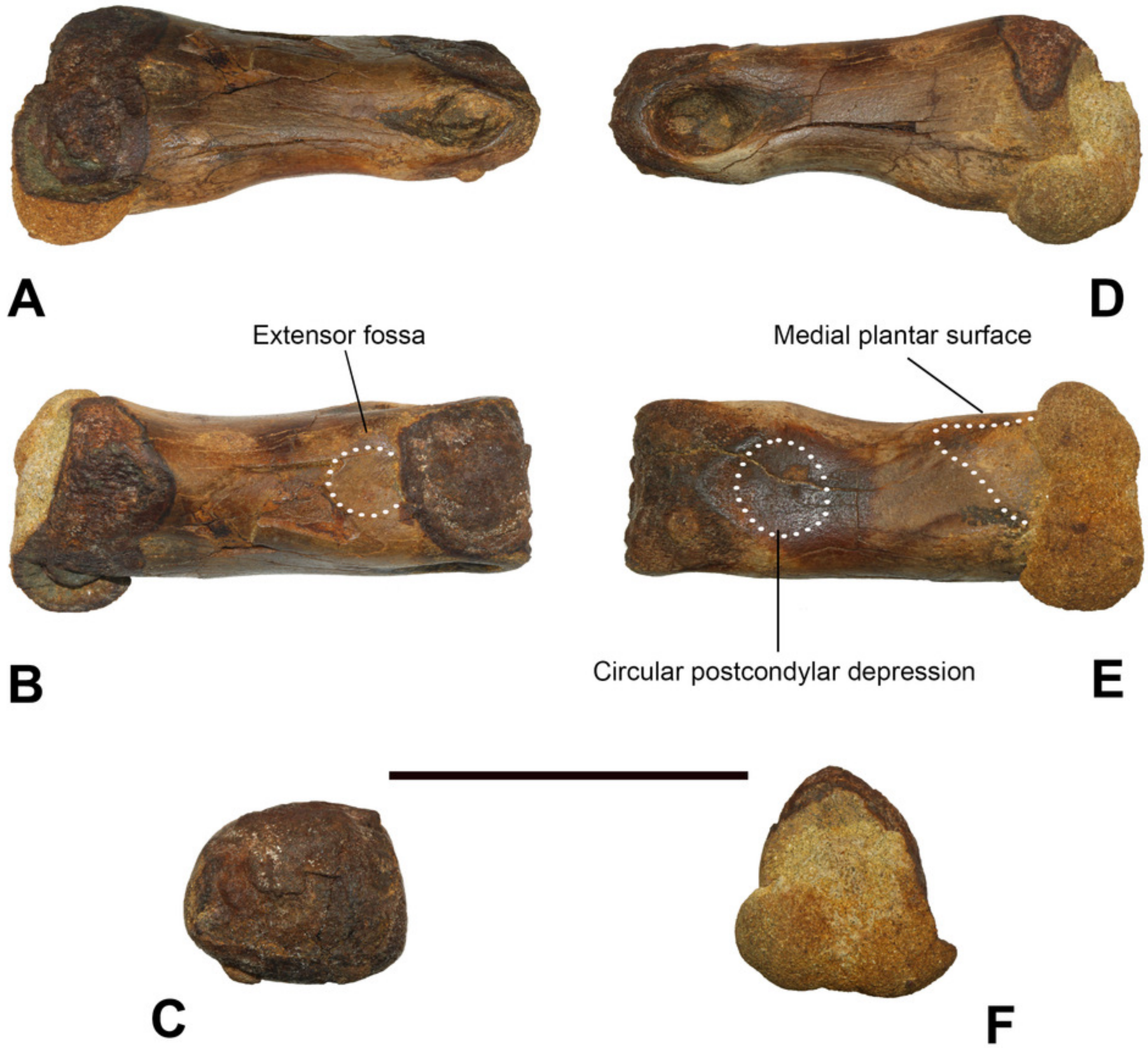
A
D
Extensor fossa
Medial plantar surface
B
Circular postcondylar depression
E
C
F

Figure 6

Iron Lightening Member phalanx, Ziebach County, South Dakota. YPM VP.061705.

(**A**) lateral, (**B**) dorsal, (**C**) distal, (**D**) medial, (**E**) ventral and **(F**) proximal views. Note that medial and lateral are tentative designations. Scale bar is 5 cm. Courtesy of the Division of Vertebrate Paleontology; Peabody Museum of Natural History, Yale University; Photography by Vanessa R. Rhue

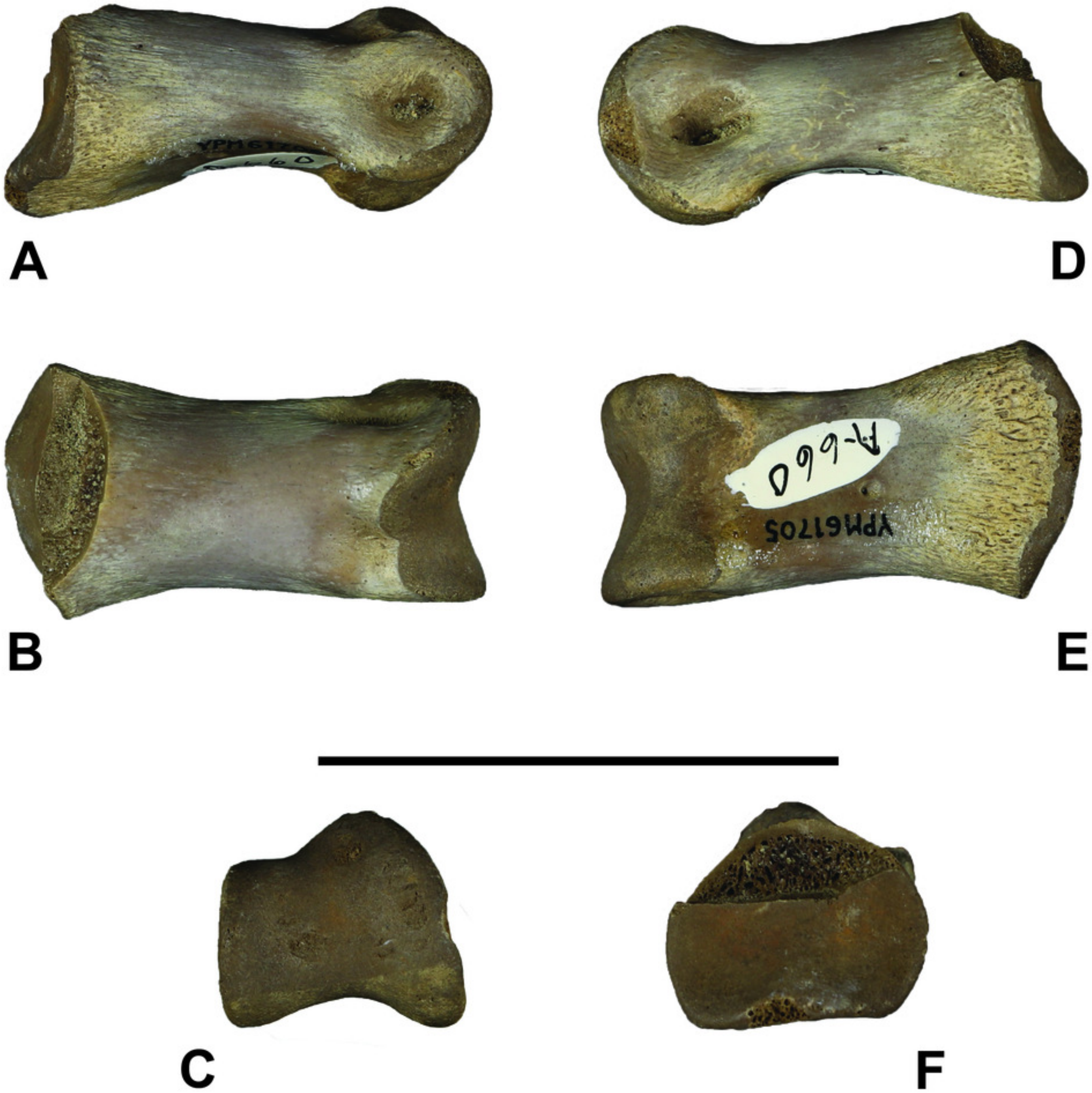
A
D
B
E
YPM61705
C
F

Table 1(on next page)

Mensuration data for theropod phalanges DMNH EPV.138575 and YPM VP.061705

Measurements in mm. O is circumference Ø is diameter. Because YPM VP.061705 could not be examined in person due to pandemic restrictions in place during this research, some measurements could not be obtained.

CHARACTER		DMNH EPV.138575	YPM VP.061705
Length	Proximodistal	80	45
Distal Width	Dorsoventral	24	19
	Mediolateral	28	22
Proximal Width	Dorsoventral	35	19
	Mediolateral	27	24
Midshaft Width	Dorsoventral	25	12
	Mediolateral	27	18
Shaft O		82	
Medial Fossa	Depth	6	
	Proximodistal Ø	15	7
	Dorsoventral Ø	11	5
Lateral Fossa	Depth	3	
	Proximodistal Ø	10	6
	Dorsoventral Ø	6	4