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Redescription of Arundel Formation Ornithomimosaur Material and a Reinterpretation of
Nedcolbertia justinhofmanni as an “Ostrich Dinosaur”: Biogeographic Implications.

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Abstract.

The fossil record of dinosaurs from the Early Cretaceous of eastern North America is scant, especially since few formations from the east are fossiliferous. Among those that are is the Arundel Formation of the eastern seaboard, which has produced among the best dinosaur faunas known from the Early Cretaceous of eastern North America. The diverse dinosaur fauna of this formation has been thoroughly discussed previously, but few of the dinosaur species originally described from the Arundel are still regarded as valid genera. Much of the Arundel material is in need of review and redescription. Among the fossils of dinosaurs from this formation are those referred to ornithomimosaurs. Here, I redescribe ornithomimosaur remains from the Arundel facies of Prince George’s County, Maryland which may be from two distinct ornithomimosaur taxa. These remains provide key information on the theropods of the Early Cretaceous of Eastern North America. Recent discoveries of small theropod material from the Arundel Formation are also reviewed and described for the first time. The description of the Arundel material herein along with recent discoveries of basal ornithomimosaurs in the past 15 years has allowed for comparisons with the coelurosaur *Nedcolbertia justinhofmanni*, suggesting the latter animal was

a basal ornithomimosaurian dinosaur rather than a “generalized” coelurosaur as which it was originally described. Comparisons between the Arundel ornithomimosaur material and similar Asian and European specimens suggest that both extremely basal ornithomimosaurs and more intermediate or derived forms coexisted throughout the northern hemisphere during the Early Cretaceous. Additionally, the possible presence of two distinct ornithomimosaurs in the Arundel allies the Arundel facies with Asian sediments in their coelurosaurian fauna.

Introduction.

The fossil record of dinosaurs from eastern North America during the Cretaceous is sparse compared that of the west of the continent, and the best dinosaur fauna known from eastern North America comes from the Arundel facies of the Potomac Group of Maryland. This unit, which is Aptian in age (Kranz, 1998), has yielded specimens of the sauropod dinosaur *Astrodon johnstoni*, the ornithopod *Tenontosaurus sp.*, the nodosaur *Priconodon crassus*, the tooth of a ceratopsian, and a number of theropods including *Deinonychus sp.* and the dubious theropods *Allosaurus medius*, *Creosaurus potens*, and *Coelurus gracilis* (Kranz, 1998; Weishampel et al., 2004; Weishampel, 2006).

Some of the first ornithomimosaur material to come from the Arundel has been the subject of some taxonomic confusion (Weishampel, 2006). Originally found by Lull (1911) to be the bones of an ornithopod he named *Dryosaurus grandis*, the ornithomimosaur specimens from the Arundel have been described as a species of *Ornithomimus* (“*O.*” *affinis*), referred to the genus *Archaeornithomimus*, regarded as a small theropod of indeterminate affinities, and finally regarded as an ornithomimosaur of indeterminate affinities (Gilmore, 1920; Russell, 1972; Smith

& Galton, 1990; Makovicky, Kobayashi & Currie, 2004; Weishampel, 2006). The metatarsal III and pedal ungual described by Gilmore (1920) were also referred to as *Ornithomimus sp.* or *Ornithomimus affinis* by Serrano-Brañas et al. (2016). However, if any of the material were to be described as a new species in the future, the original species name (*grandis*) given by Lull (1911) would take priority.

Gilmore (1920) originally described the Arundel material as then a new species of ornithomimosaur based on some pedal elements and caudal vertebrae. Additionally, Weishampel and Young (1996) noted that pedal elements and the proximal portion of a tibia were retrieved in 1992. These are in the collections of the United States National Museum of Natural History. Most recently, an astralagus was recovered from Prince George's County, Maryland in 2010 (USNM PAL540727). Additional material has also been recovered recently from the Arundel but never have been formally described until now.

Early Cretaceous ornithomimosaur remains have been retrieved from from Western North America (Ostrom, 1970; Galton & Jensen, 1975), Europe (Sanz & Wenz, 1988; Perez-Moreno et al., 1994; Neraudeau & Allain, 2012; Allain et al., 2014), Asia (Maleev, 1954; Dmitiriev, 1960; Kalandadze & Kurzanov, 1974; Hasegawa & Manabe, 1986; Xu & Wang, 1999; Boonchai & Grote, 2009; Ji et al., 2003; Molnar & Obata, 2009; Buffetaut, Suteethorn & Tong, 2009; Makovicky et al., 2009; Jin, Chen & Godefroit, 2012), and Africa (Choiniere, Forster & De Klerk, 2012). The rich fossil record of Early Cretaceous ornithomimosaur which has developed in the past decade has allowed for comparisons of the Arundel specimens with a multitude of new taxa.

Here, I redescribe the theropod remains assigned to ornithomimosaur which were retrieved from the Arundel Formation of Maryland and housed in the collections of the United States National Museum and those of Dinosaur Park, Maryland. Gilmore (1920) related that the site where the material of “*Dryosaurus*” *grandis* was found was near Muirkirk, which matches with the site of the Maryland Dinosaur Park locality. Indeed, material from this latter site and the site by Muirkirk are both labeled as coming from site number 41615 in the collections of the United States National Museum.

The Arundel ornithomimosaur material has implications for the evolution of more derived members of the ornithomimosauria, suggesting that they were present across North America during the Early Cretaceous. However, the lack of material able to be assigned to a single animal means that any naming of a new Arundel taxon or new taxa must wait until a skeleton is recovered which can be confidently thought of as formed by associated material. Additionally, a reinterpretation of *Nedcolbertia justinhofmanni* from the Early Cretaceous of Utah as an ornithomimosaur is provided, showing that taxa with no arctometatarsalian pes and a likely near-arctometatarsalian pes coexisted during relatively the same time in North America as they did in Asia. The biogeographic and ecological implications of ornithomimosaur with likely different metatarsus morphologies coexisting in North America are discussed, though the paucity of material from these North American forms during the Early Cretaceous makes any conclusions limited. This suggests that the basal and derived features found in the Arundel ornithomimosaur material may be indicative that two or more species of ornithomimosaur existed in the Arundel, as seen in the Early Cretaceous Yixian Formation of China (Ji et al., 2003; Ji, Chen & Godefroit, 2012).

Methods.

Permits.

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

Help in accessing the specimens in the National Museum of Natural History was given by Mr.

Thomas Jorstad of the Smithsonian Institution, while help in accessing the collections of the

Parks and Recreation of Prince George's County from Dinosaur Park was given by Mr. Benjamin

Miller.

Institutional Abbreviations.

I use the term USNM V to refer to the vertebrate zoology collections and USNM PAL to refer to

the paleontology collections of the United States National Museum. I use the term NHRD-AP to

refer to the National and Historical Resources Division Archaeology Program collections of

fossils from Dinosaur Park, Maryland.

Results.

Geological Setting.

The best record of ornithomimosaur material from the Arundel comes from a site numbered 41615 in the USNM collections (=the Dinosaur Park site near Muirkirk). This site is in Prince George's County, Maryland and pertains to the Arundel facies. This lithology of the Arundel was often described as "blue charcoal clays with iron carbonate nodules" (Kranz, 1998).

However, some have doubted the placement of the sediments originally referred to as the Arundel as a formation and instead have suggested that they constitute as deposits from oxbow swamps. This interpretation is based on the observation that the clays of the Arundel appear as discontinuing elongated sediments (Kranz, 1998). Additionally, the palynomorphs of the Patuxent Formation and the Arundel cannot be distinguished (Brenner, 1963; Doyle & Hickey, 1976; Doyle & Robbins, 1977; Robbins, 1991; Kranz, 1998), providing further evidence against the designation of the Arundel as a distinct geological unit. Lipka et al. (2006) regarded both the Arundel and Patuxent as facies within the larger Potomac Formation. The sediments referred to as the Arundel are Aptian in age and have produced a diverse vertebrate fauna, including saurischian & ornithischian dinosaurs, testudines, anurans, the shark *Hybodus*, and the lungfish *Ceratodus* (e. g. Kranz, 1998; Weishampel et al., 2004; Weishampel, 2006).

Systematic Paleontology.

Dinosauria Owen 1852 sensu Padian and May 1993

Theropoda Marsh 1881 sensu Gauthier 1986

Ornithomimosauria indet. Barsbold 1976 sensu Choiniere, Forster & De Klerk 2012

Material: USNM V8454, a dorsal vertebral centrum; USNM V5701 & USNM V6116, two caudal vertebra; USNM PAL466054, the proximal portion of a tibia and a pedal phalanx and an ungual; USNM 5652 and USNM PAL5407, left and right astragali; USNM V5684, the distal portion of metatarsal III; USNM V5704, the distal portion of metatarsal II; USNM V6108 & USNM V5453, pedal phalanges II-1; USNM V5703, pedal phalanx III-2; USNM V6115, phalanx from pedal digit IV; USNM V6107, a pedal ungual, all recovered from site 41615 near

Muirkirk, Maryland and in the collections of the National Museum of Natural History ; ?USNM V8456 & ?USNM V16748, recovered elsewhere in Prince George's County but also in the aforementioned collection. NHRD-AP 2015.v.1039 includes the proximal and distal ends of a humerus, NHRD-AP 2015.s.507 and 2013.s.503, appendicular fragments; NHRD-AP 2016.s.600, NHRD-AP 2016.s.576, NHRD-AP 2016.s.560, and NHRD-AP 2015.v.1028, vertebrae; NHRD-AP 2016.s.560, NHRD-AP 2015.s.539, pedal phalanges; NHRD-AP 2014.s.195, NHRD-AP 2014.s.196, NHRD-AP 2014.s.197, NHRD-AP 2014.s.198, NHRD-AP 2016.v.1104, pedal unguals. Indeterminate appendicular elements, including possible limb shafts, were recovered from the Muirkirk site (NHRD-AP 2015.s.507, NHRD-AP 2013.s.503, and three unnumbered specimens), but cannot be confidently assigned to ornithomimosaur or theropods.

Description: The proximal and distal ends of a humerus were recovered from the Dinosaur Park site, and are both somewhat eroded. They are similar in morphology to the characteristics of ornithomimosaur humeri listed by Makovicky, Kobayashi & Currie (2004) in having small deltapectoral and bicipital crests and having a relatively straight shaft. The morphology of this humerus compares especially well to that of *Harpymimus* (figure 6.4E in Makovicky, Kobayashi & Currie, 2004).

The dorsal vertebral centrum (figure 2A-B) that was recovered from site 41615 and assigned to an ornithomimosaur by Gilmore (1920) is slightly worn and opisthocoelus, though the proximal face is almost flat in lateral view. The vertebra measures 7.6 cm long anteroposteriorly and 49.5 millimeters wide as measured mediolaterally along its distal face (Gilmore, 1920). The neural arch of USNM V8454 was broken off right at the neurocentral

suture, the outline of which is still completely visible in lateral and dorsal view on the dorsal face of the vertebra. Gilmore (1920) originally regarded the vertebra as the vertebra directly in front of the sacrum of an ornithomimosaur based on comparisons with “*Ornithomimus*” sedens. The condition of the dorsal face suggests that the suture was not fused and therefore that the dinosaur to which USNM V8454 pertains was a juvenile or subadult during the time of its death. However, beyond the fact that the vertebra was recovered from site 41615 and shares with ornithomimosaur dorsal vertebrae a feature in being nearly or completely platycoelous. However, the vertebra could easily belong to another species of theropod or dinosaur. Additionally, a few other vertebrae were more recently recovered from the Muirkirk site (e. g. figure 1B), though these may belong to other theropods or dinosaurs.

Both caudal vertebra (figure 2A-B) originally referred to ornithomimosaur are elongate. USNM V5701 is opisthocoelus and has an elongated neural spine which is eroded in its middle, and measures 68.7 mm anteroposteriorly, while USNM V6116 is 67.5 mm long (Gilmore, 1920). Two elongated prezygapophyses extend distally past the border of the vertebral centrum, though according to Gilmore (1920) should be longer and were not restored to their correct length. the ventral surface of USNM 5701 arches slightly in the middle of the ventral face. USNM V6116 is similar to USNM V5701, but is stouter and its broken prezygapophyses do not extend past the distal end of the centrum. Unfortunately, the distal and proximal ends of USNM V6116 are badly cracked. Both vertebra, as Gilmore (1920) noted, are similar to the distal caudal vertebrae of ornithomimosaur in their extremely elongated nature and extremely elongated prezygapophyses.

The proximal end of the tibia figured in Weishampel & Young (1996) is well preserved and retains a large cnemial crest, as in ornithomimosaur (Makovicky, Kobayashi & Currie, 2004). Additional restoration of this element has gone on presumably after Weishampel (1996), as the new attached medial portion of the fibula is absent in their figure, which is the element in medial view. The proximal most portion of this ornithomimosaur tibia was preserved and is widened due to being the area at which the fibular crest extended proximally. This tibia indicates the presence of a medium-sized ornithomimosaur.

The left and right astragali (figure 3A-D) retrieved from site 41615 are similar in form in having an ascending process which is square in posterior and anterior views which is separated by a very shallow oval depression from the condylar bodies of the astragali. USNM V5652, the left astragalus, is slightly longer than the right astragalus USNM PAL5407 at 78 mm long anteroposteriorly and 56 mm tall, though this can be attributed to the erosion present on the latter 70 mm long, 40.125 mm tall specimen. The left astragalus narrows medially in dorsal and ventral view only to become expanded again below the ascending process, which Gilmore (1920) noted had been worn down, and calcaneal facet. This feature was also noted by Gilmore (1920). A sulcus also separates the astragalar condyles in USNM V5652. Makovicky, Kobayashi & Currie (2004) noted that a shallow sulcus separating the astragalar condyles is found in ornithomimosaur. These features are faint in USNM PAL5407, which has a shorter ascending process that may have been partially distorted during preservation to orient outward from the main body of the astragalus in dorsal view. USNM V5652 is notably heavily stabilized though is similar in original color to USNM PAL5407 and the other specimens from site 41615.

Portions of metatarsals II & III (figure 4A-B) were also recovered from site 41615 and described by Gilmore (1920). Metatarsal III is elongate and measures 139.5 mm long anteroposteriorly. At its distal end, metatarsal III measures 43 mm wide, while 75 mm towards its proximal end, it measures only 29 mm in width (Gilmore 1920). Both collateral ligament pits of metatarsal III are large and teardrop-shaped. The presence of an arctometatarsalian condition in ornithomimosaur to which USNM 5684 pertains is supported by the thinning of metatarsal III immediately after this diaphysis “bulge”. This is found in the ornithomimosaur taxa *Struthiomimus*, *Gallimimus*, *Ornithomimus*, and somewhat in *Archaeornithomimus*, *Harpymimus*, and *Nqwebasaurus* (figure 6; figure 6.5F-H in Makovicky, Kobayashi & Currie, 2004; figure 14B in Choiniere, Forster & De Klerk, 2012). In fact, metatarsal III is almost an exact match with metatarsal III of *Ornithomimus velox* YPM VP 000542 (figure 6). Ventrally, the distal condyles are separated, though in dorsal view they are fused. Both collateral ligament pits of metatarsal III are large and teardrop-shaped. The distal end of metatarsal II which was collected preserves collateral ligament pits and curves outward from the center of the pes to allow room for the articulation of metatarsal III, a feature also found in ornithomimosaurs and most notably in *O. velox* YPM VP 000542. This portion of metatarsal II measures 54 mm anteroposteriorly and is distally 33 mm wide.

A number of phalanges are preserved, including two which Gilmore (1920) regarded as both being the proximal phalanx of left pedal digit II. These two specimens (figure 6A-B) are similar in being elongate, having distal condyles noticeably separated by a groove, having circular collateral ligament pits, having a slight depression at the distal end of their dorsal faces, and finally having a concave proximal articular facet bordered by a slight rim. This last feature,

however, is less noticeable in USNM V6108. USNM V5453 and USNM V6108 measure 82 mm and 79 mm at their centers and 34 mm and 32 mm wide as measured mediolaterally along their proximal faces, respectively (Gilmore, 1920). These specimens compare very well with other ornithomimosaurian taxa (Gilmore, 1920; Buffetaut, Suteethorn & Tong, 2009; Serrano-Brañas et al., 2016), and compare especially well with pedal phalanx II-1 of *Gallimimus bullatus* and *Struthiomimus altus* in having condyles noticeably separated by a deep groove, a slightly expanded rim around the proximal articular facet, and a slight fossa at the distal end of their dorsal faces. These two phalanges are similar in color to metatarsal II and III from site 41615 and somewhat to caudal vertebra USNM V5701. These similarities in morphology suggest that the two pedal phalanges II-1 are of ornithomimosaur origin.

A pedal phalanx regarded as III-2 by Gilmore (1920) was also found at site 41615 (figure 6C). Both collateral ligament pits were preserved and are teardrop-shaped. As in phalanges II-1 of site 41615 a slight depression appears at the distal end of the dorsal face of USNM V5703. This phalanx is very slightly curved and has a noticeably expanded rim surrounding the proximal articular facet, which Gilmore (1920) regarded as warranting the phalanx's position as III-2. The color of the specimen is somewhat similar to USNM V6116 and metatarsal III from sight 41615. Indeed, the phalanx is very similar to III-2 of *Ornithomimus* (Gilmore, 1920) and *Struthiomimus*, but less so to that of the basal taxon *Harpymimus* in being less robust (figure 6.5F-H in Makovicky, Kobayashi & Currie, 2004), suggesting that the presence of expanded rim around the proximal articular facet on an elongate pedal phalanx III-2 is a derived trait among ornithomimosaur. The specimen has an anteroposterior length of 69 mm and is 32 mm wide as measured mediolaterally along its proximal face (Gilmore, 1920).

A partial phalanx, USNM V6115 (figure 6D), was recovered from site 41615 and is interpreted as coming from digit IV of the pes of a theropod dinosaur due to the immediate proximodorsal curvature of the dorsal and ventral faces of the specimen in lateral and medial view suggesting an anteroposteriorly short phalanx. The collateral ligament pits are not well-preserved though still are somewhat visibly circular. The specimen is 31 mm long anteroposteriorly. Though the specimen does indeed share a synapomorphy with ornithomimosaur pedal phalanges from digit IV in being anteroposteriorly shortened with its proximal and distal faces close together, this feature is also found in a variety of other theropods.

NHRD-AP 2015.s.539 (figure 6G-H) is much more well preserved and is interpreted as pedal phalanx IV-1 of an ornithomimosaur due to its anteroposteriorly short morphology where the distal and proximal faces are close together combined with its size. The dorsal and ventral faces jut out noticeably above and below the proximal articular facet, the distal condyles are strongly separated, and the collateral ligament pits are circular and deep.

Two morphotypes of pedal ungual have been recovered from the Dinosaur Park site (site 41615). USNM V6107, a pedal ungual (figure 7A), was recovered from site 41615 and described by Gilmore (1920). In lateral and medial views, USNM V1607 is very slightly curved. The pedal ungual bears a flexor fossa on the proximal end of its ventral face, a synapomorphy of ornithomimosauria (Choiniere, Foster & De Klerk, 2012). As in ornithomimosaur (Makovicky, Kobayashi & Currie, 2004), the specimen bears deep grooves for the claw sheath which taper anteromedially along the specimen towards the tip. This pedal claw measures 55.5 mm long anteroposteriorly and 17 mm wide mediolaterally along its proximal articular facet (Gilmore, 1920). The specimen is most similar to the pedal ungual of *Struthiomimus altus* figured in

Serrano-Brañas et al. (2016). Another pedal ungual, NHRD-AP 2014.s.197 (figure 7B), was recovered from the Dinosaur Park site and is very similar to USNM V6107. Both unguals are not elongate, are recurved, and have prominent rims around their proximal articular facets. This morphology is unlike that of NHRD-AP 2016.s.196, NHRD-AP 2014.s.198, NHRD-AP 2016.v.1104, and NHRD-AP 2014.s.196 (figure 7C-F), which are larger than USNM V6107 and NHRD-AP 2014.s.197, have more pronounced grooves for the claw sheath, are less recurved, and do not have noticeable rims surrounding their proximal articular facets. These two claw morphotypes are indicative that two ornithomimosaur taxa are present at the Dinosaur Park site.

The two phalanges discovered elsewhere in Prince George's County, Maryland are both interpreted as phalanges of digit IV of a theropod as they are both anteroposteriorly short. This is notably characteristic of digit IV of ornithomimosaur (Choiniere, Foster & De Klerk, 2012). USNM V8456, which Gilmore (1920) originally referred to the Arundel ornithomimosaur, is 38 mm long anteroposteriorly and 24 mm wide mediolaterally along its proximal face (figure 6E-F). USNM V16748 is similar in size and complete. Both preserve circular collateral ligament pits and unfused distal condyles, and are tentatively assigned to the Arundel ornithomimosaur of site 41615 due to their similarities with the known pedal phalanx from digit IV found at site 41615 and comparatively short geographic distance between the locations where the two phalanges were each found at site 41615.

Discussion.

The Muirkirk Arundel ornithomimosaur material represents among the most complete records of any dinosaur group from the Early Cretaceous of eastern North America. Importantly,

the distal end of metatarsal III assigned to an ornithomimosaur may exhibit a feature unique to the specimen among ornithomimosaurs. The dorsal surface of the distal end of metatarsal III displays two ridges which migrate towards each other from the lateral and medial ends of the dorsal face of metatarsal III to form a distinct, upside-down V-shaped outline. These ridges then run almost parallel to each other and then depart again to the lateral and medial sides of the dorsal face. The distal condyles of metatarsal III are also fused in dorsal view, unlike the condition found in *Tototlmimus packardensis* (figure 6 in Serrano-Brañas et. al., 2016). Notably, the ornithomimosaur material from site 41615 may belong to multiple theropod species. However, all share morphological affinities with ornithomimosaurs. The tibia discovered at the Muirkirk site can be distinguished from other theropods, excluding tyrannosaurids and *Allosaurus*, by having a large cnemial crest to which an accessory process is laterally adjacent (Makovicky, Kobayashi & Currie, 2004). Neither tyrannosaurids or *Allosaurus* are known from the Arundel, and the tibia is smaller than those of the aforementioned two taxa. The metatarsals from site 41615 are dissimilar to the simplistic cylindrical metatarsals of *Dilong* (figure 6K) and non-arctometatarsalian metatarsals of other Early Cretaceous tyrannosaurs of similar size. The metatarsals are also more robustly built than those of compsognathids, and unlike dromaeosaurs the metatarsus is not shortened. Additionally, the portion of metatarsal III recovered does not suddenly shrink directly after it becomes expanded towards its diaphysis as in arctometatarsalian tyrannosauroids (e. g. figure 5.20 in Holtz, 2004) and troodontids (e. g. figure 9.6 in Makovicky & Norell, 2004). The phalanges of digit II are more elongate than in most troodontids (e. g. figure 9.6 in Makovicky and Norell, 2004). The phalanges II-1 and unguals from the Muirkirk site can be distinguished from dromaeosaurs and troodontids in not having their condyles

dorsally oriented to account for II-2 to be raised with a hypertrophied claw and lack a visible flexor tubercle, respectively. The latter feature also distinguishes the pedal ungual found at site 41615 from that of compsognathids. The majority of the theropod material previously referred to “ostrich dinosaurs” from the Muirkirk site can be placed within ornithomimosauria indet. and some possibly even to ornithomimidae indet. due to having a single flexor fossa on the pedal unguals, anteroposteriorly short phalanges from pedal digit IV, pedal unguals triangular in cross-section, a likely arctometatarsalian pes, and relatively straightened edges on the ventral surface of the pedal unguals (Barsbold & Osmólska, 1990; Choiniere, Forster & De Klerk, 2012). However, the two morphotypes discussed herein suggest that at least two taxa were present. The ornithomimosaur to which the recovered metatarsal III and pedal phalanx III-2 pertains were likely intermediate forms, while those to which the humerus discussed herein and the pedal unguals USNM 6107 and NHRD-AP 2014.s.197 belong to were likely more basal based on the similarities of the humerus to *Harpymimus* and the recurved morphology of the pedal unguals, which is unlike the straightened and elongate pedal unguals of ornithomimids. To this latter morphology the majority of the pedal unguals retrieved from the Dinosaur Park site are more akin.

Redescription of the Arundel ornithomimosaur material and the naming of new basal ornithomimosaur taxa in recent years has allowed for the reinterpretation of the “generalized” North American coelurosaur *Nedcolbertia justinhofmanni* as an ornithomimosaur. *Nedcolbertia* shares three synapomorphies with ornithomimosaur in having anteroposteriorly shortened phalanges from pedal digit IV, the ventral surfaces of the pedal ungual flattened in lateral view, and a single flexor fossa on the proximal end of the ventral surface of its pedal unguals (figure 8

& figure 9 in Kirkland et. al., 1998; Choinere, Forster & De Klerk, 2012). The proximal end of metatarsal III is restricted mediolaterally in a very similar fashion to *Harpymimus*, and in proximal view the metatarsals are similar in shape to those of *Kinnareemimus* (figure 8 in Buffetaut, Suteethorn & Tong, 2009). The pedal unguals of *Nedcolbertia* are also triangular in cross-section (Kirkland et. al., 1998), a feature listed as a synapomorphy of Ornithomimosauria by Barsbold & Osmólska (1990). Importantly, the classification of *Kinnareemimus* as an ornithomimosaur was thought to be tentative by Brusatte et al. (2014). Yet *N. justinhofmanni* displays multiple other features found in ornithomimosaur, including a proximally pinched metatarsal III which is not limited to the plantar half of the foot as in tyrannosauroids (Holtz, 2004) and not restricted to the extent seen in troodontids (Makovicky & Norell, 2004), elongated caudal vertebra, elongated pedal unguals with deep grooves for the claw sheath, a tall ascending process on the astragalus, a complex space on the lateral side of the astragalus into which the calcaneum fits, a sulcus separating the astragalar condyles, and no sulcus separating the femoral head from the greater trochanter (figure 8D-N, figure 9B, figure 6C-E in Kirkland et al., 1998).

Unlike some ornithomimosaur, the flexor tubercle of the first manal ungual is extremely pronounced, the manal unguals are likely differentiated, and the dorsal vertebrae are simplistic and pneumatic in *Nedcolbertia* (Kirkland et. al., 1998). The morphology of the manal unguals of *Nedcolbertia* is indeed similar to the basal ornithomimosaur *Nqwebasaurus* and *Harpymimus* in having large flexor tubercles on the manal unguals. Additionally, *Nedcolbertia* and *Nqwebasaurus* can be linked by having slender pedal unguals, though this is less pronounced in the former taxon. The astragali are also morphologically similar in *N. justinhofmanni* and *N. thwazi* in the relative height of their ascending processes. *N. justinhofmanni* can be differentiated

from the some of the Arundel material by having straighter, more elongate pedal unguals and lacking the visibly separated distal condyles seen in phalanx II-1 of the latter taxon (figure 8 & figure 9 in Kirkland et. al., 1998). Additionally, *N. justinhofmanni* can be distinguished from Arundel ornithomimosaur likely can be differentiated in the morphology of their metatarsus, as the known portion of metatarsal III of the site 41615 ornithomimosaur suggests that at least one ornithomimosaur taxon found at the Arundel had a near-arctometatarsalian condition similar to that of *Kinnareemimus*, while in *Nedcolbertia* the dorsal face of metatarsal III is still completely visible along the entire portion of the metatarsus. *Nedcolbertia* is therefore considered as a basal ornithomimosaur due to its non-arctometatarsalian pedal condition where the shaft of metatarsal III is at least partially visible along its entire run in dorsal view.

The similarities between the Arundel ornithomimosaur metatarsal III and the Asian taxa *Harpymimus* and *Kinnareemimus* (as well as derived North American and Asian ornithomimosaur from the Late Cretaceous) and their close temporal appearance in their respective formations suggest that ornithomimosaur with a metatarsal morphology intermediate between that of the basal *Nqwebasaurus thwazi* and the derived condition seen in ornithomimids were present in Asia and through the whole of North America. *Kinnareemimus* and *Nedcolbertia* come from post-earliest Cretaceous pre-Aptian (possibly Barremian) and Barremian sediments, respectively (Kirkland et. al., 1998; Buffetaut, Suteethorn & Tong, 2009), while the Arundel Formation from which the metatarsal III of an ornithomimosaur discussed herein pertains is Aptian in age (Kranz, 1998). *Harpymimus* is from Albian deposits (Makovicky & Currie, 2004). This temporal frame suggests that both basal ornithomimosaurians lacking an arctometatarsalian or near-arctometatarsalian pes and ornithomimosaur with a pedal morphology extremely close

to the arctometatarsalian condition may have coexisted in North America during the mid-Early Cretaceous. Additionally, ornithomimosaur metatarsals from the Late Aptian to Early Albian Cloverly Formation of the American west (Ostrom, 1970) have morphologies consistent with a near-arctometatarsus or arctometatarsus, supporting the presence of an ornithomimosaurian lineage with a near-arctometatarsalian or arctometatarsalian pes in western North America. Unfortunately, only portions of metatarsals II & III of this Cloverly Formation form are known (Ostrom 1970). The European taxon *Valdoraptor* and an as-yet-unnamed species from the Angeac bone bed of France from the Early Cretaceous also have extremely similar metatarsals to the Arundel material though do not share the mediolaterally expanded condition near the diaphysis of metatarsal III and also can be differentiated from the Arundel material by having a mediolaterally compressed metatarsal II (Naish, 2011; Allain et al., 2014). These three taxa are similar in having the distal end of metatarsal II medially projected (figure 4B; figure 6B; Naish, 2005; Allain et al., 2014). It therefore seems plausible that both basal ornithomimosaurs sharing such features as an only slightly pinched proximal metatarsal III, large flexor tubercles on their manal unguals, and similar astragali and ornithomimosaurs with a more derived metatarsus morphology which included a mediolateral expansion of metatarsal III towards its diaphysis, an elongate pedal phalanx III-2 with a noticeably expanded rim surrounding the proximal articular facet, flattened pedal unguals in most cases not as elongated as seen in *N. justinhofmanni* and *Nqwebasauurus thwazi*, and strongly separated condyles on phalanx II-1 both had become geographically widespread during the Early Cretaceous. This is consistent with the findings of Allain et al. (2014) and the placement of *N. justinhofmanni* as an ornithomimosaur shows that the ornithomimosaurs were also found across North America during the Early Cretaceous in

addition to Europe and Asia (Allain et al., 2014). Importantly, the two taxa represented by distinct morphotypes of pedal ungual found at the Arundel may each be associated with one of these ornithomimosaur lineages. However, associated ornithomimosaur material will have to be recovered from the Arundel facies before any educated judgement can be made as to their affinities.

Conclusions.

The Arundel ornithomimosaur represented at site 41615 are some of the most well-known theropods from the Early Cretaceous of eastern North America. Furthermore, the Arundel material along with recently described ornithomimosaur have provided evidence for the placement of *Nedcolbertia justinhofmanni* as an ornithomimosaur. Both the Arundel material and *Nedcolbertia* have implications for the biogeography of Early Cretaceous ornithomimosaur lineages, suggesting that extremely basal and more derived ornithomimosaur had a wide biogeographic range during the Early Cretaceous and may have coexisted in at least Asia and North America.

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A.



B.



Figure 1. Proximal and distal ends of the humerus of an Arundel ornithomimosaur NHRD-AP 2013.v.1039 in lateral (A, B) view. Courtesy M-NCPPC.

A.



B.



C.



Figure 2. Selected dorsal vertebra of the Arundel ornithomimosaur in lateral (A, B.), and dorsal (C) views. USNM V8454 in A, D; Scale bar = 50 mm (A, C); =20 mm (B). A, F courtesy of Smithsonian Institution. Photos by M. Brett-Surman. B-E courtesy M-NCPPC.

A.



B.



Figure 3. Caudal vertebra of Arundel ornithomimosaur in lateral (A, B) view. Scale bar = 60 mm. USNM V5701 pictured in A; USNM V6116 pictured in B. Courtesy of Smithsonian Institution. Photos by M. Brett-Surman.

A.



B.



C.



D.



Figure 4. Left and right astralagi of Arundel ornithomimosaur in medial (A, C) and dorsal (B, D) views. Scale bar = 60 mm. USNM PAL5407 pictured in A-B; USNM V5652 pictured in C-D. Courtesy of Smithsonian Institution. Photos by M. Brett-Surman.



Figure 4. Distal tibia (A) and metatarsals II (B) and III (C) of the pes of the Arundel ornithomimosaur in medial (A) and dorsal (B, C) view. Scale bar = 100 (B, C). Courtesy of Smithsonian Institution. Photos by M. Brett-Surman.

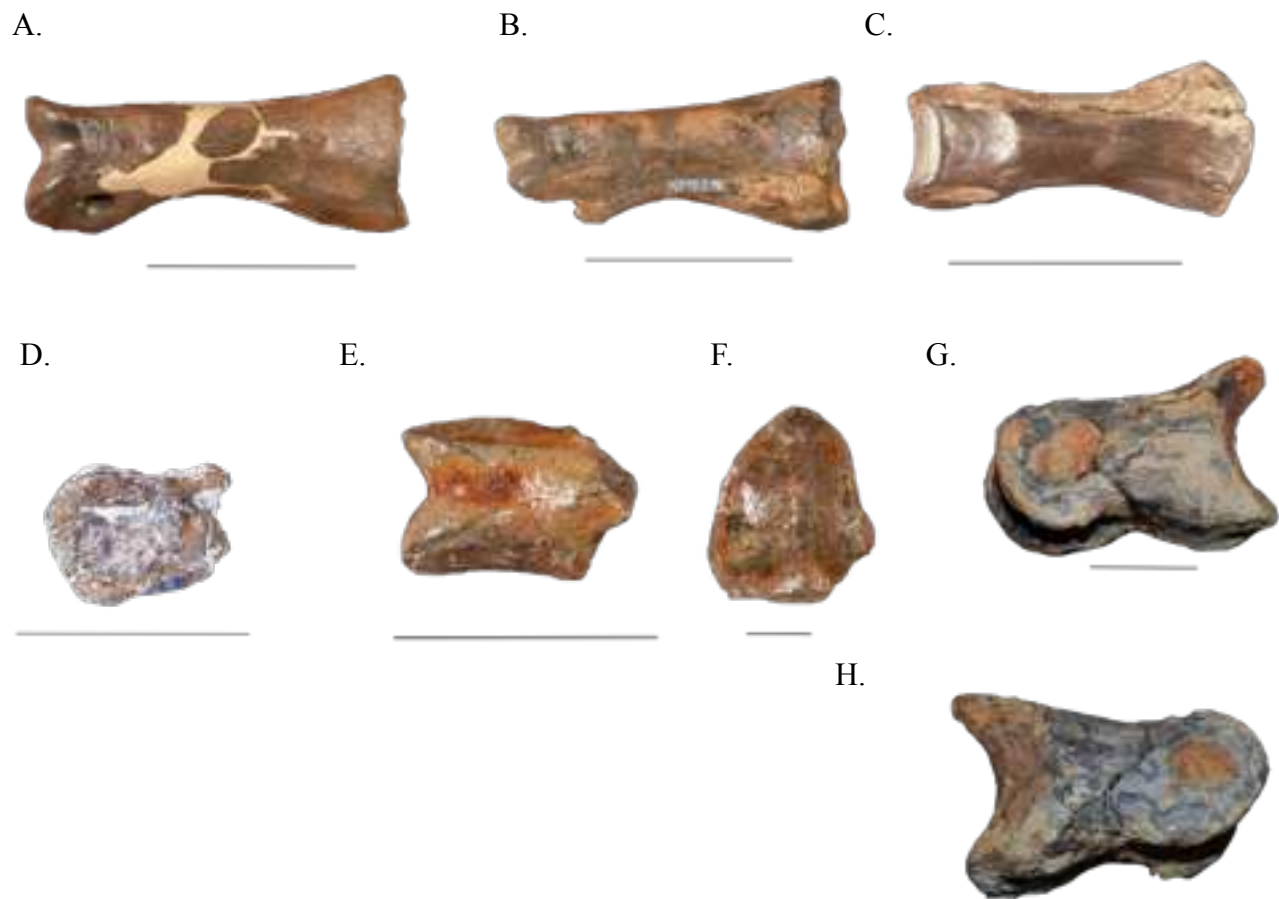


Figure 6. Pedal phalanges from Arundel ornithomimosaur. USNM V5453, right pedal phalanx II-1, in dorsal view (A); USNM V6108, ?right pedal phalanx II-1, in dorsal view (B); USNM V5703, right pedal phalanx III-2, in dorsal view (C); USNM V6115, pedal phalanx of digit IV, in medial view (D); USNM V8456, pedal phalanx of digit IV, in dorsal (E) and proximal (F) views; NHRD-AP 2015.s.539, pedal phalanx IV-1, in ?medial (G) and ?lateral (H) views. Scale bar = 50 mm (A, B, C), = 40 mm (D, E), = 10 mm (F), =19.03 mm (G-H); = A-F courtesy of Smithsonian Institution. Photos by M. Brett-Surman. G-H courtesy M-NCPPC.

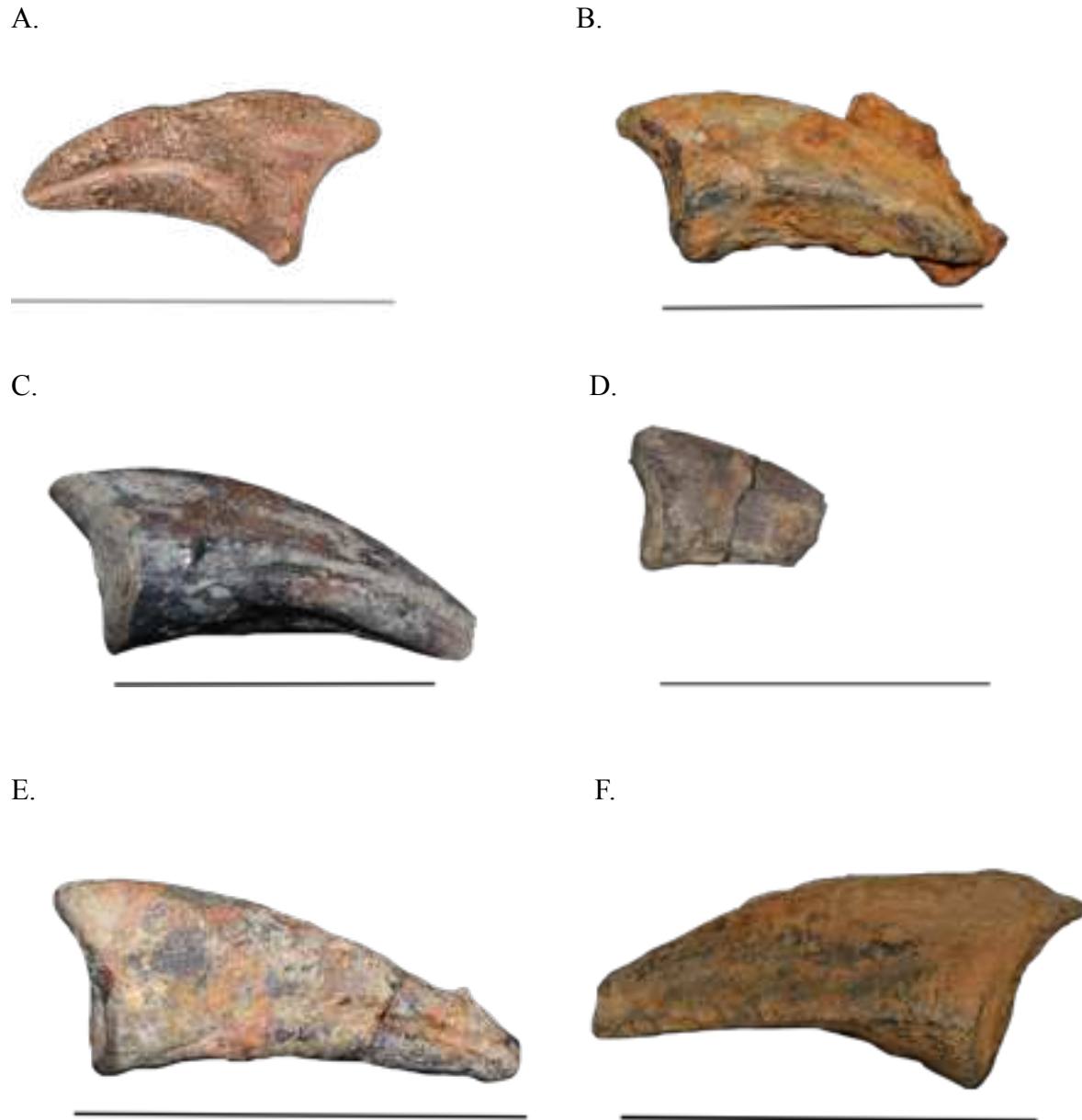


Figure 7. Pedal unguals of Arundel ornithomimosaurids in ?medial (A, F) and ?lateral (B-E) views. USNM V6107 pictured in (A), NHRD-AP 2014.s.197 pictured in (B), NHRD-AP 2016.s.196 pictured in (C), NHRD-AP 2016.v.1104 pictured in (D), NHRD-AP 2014.s.196 pictured in (E), NHRD-AP 2014.s.198 pictured in (F). A courtesy of the Smithsonian Institution. Photos by M. Brett-Surman. B-F courtesy M-NCPPC.